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THE ANATOMY AND RELATIONSHIPS OF *STEGOCERAS VALIDUS* LAMBE (REPTILIA: ORNITHISCHIA) FROM THE JUDITH RIVER FORMATION OF ALBERTA

by

© HANS-DIETER SUES

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF GEOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE ANATOMY AND RELATIONSHIPS OF *STEGOCERAS VALIDUS* LAMBE (REPTILIA: ORNITHISCHIA) FROM THE JUDITH RIVER FORMATION OF ALBERTA submitted by Hans-Dieter Sues in partial fulfillment of the requirements for the degree of Master of Science.

Richard C. Fox
(Supervisor)

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Date 31 March 1977

ABSTRACT

As a part of a revision of the North American pachycephalosaurid dinosaurs (Reptilia: Ornithischia), the species *Stegoceras validus* Lambe, 1902 has been restudied. An incomplete skeleton with an excellently preserved skull in the collections of The University of Alberta permits a reconstruction of the osteology of this taxon. Restorations of the musculature, especially of the jaw and nuchal muscles, have been attempted.

A functional analysis of the cranial architecture indicates that the thickened frontoparietal probably served as a weapon in intraspecific combat. Forces resulting from impacts could have been transmitted through the lateral wall of the unusually well ossified braincase to the occipital condyle and over the vertebral column backwards. A well-developed nuchal ligament and the powerful nuchal musculature may have aided in shock absorption.

The description and functional study provides evidence that *Stegoceras* was an herbivorous, bipedal reptile, lacking cursorial adaptations, with a broad thorax and abdomen and heavy tail. Galton's derivation of the Pachycephalosauridae from Jurassic hypsilophodontids is corroborated.

Only two species of North American pachycephalosaurids are recognized: *Stegoceras validus* and *Pachycephalosaurus wyomingensis* (Gilmore, 1931). No good evidence for close relationships to the Ankylosauria and Ceratopsia has been found.

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INTRODUCTION

1. Previous work on pachycephalosaurid dinosaurs

In 1902, Lambe described and figured two frontoparietals from the "Belly River series" (Judith River Formation (according to McLean 1971)) of Alberta as representing a new dinosaur, *Stegoceras validus*, possibly referable to the Ceratopsia. He suggested (1902: 69) that the bones were prenasals. Nopsca (1903: 266), interpreting these specimens as frontals and fused nasals, envisaged *Stegoceras* as a dinosaurian "unicorn" and compared it with the Pleistocene rhinocerotid *Elasmotherium*. He was uncertain as to the relationships of *Stegoceras*: "Ob es den *Ceratopsiden* oder *Stegosauriden* (im weiteren Sinne) zugetheilt werden muss, erscheint nach dieser neuen Deutung noch durchaus fraglich" (Nopsca 1903: 267). Lambe (1904: 24) fully agreed with Nopsca's anatomical interpretations. Hatcher (in Hatcher, Marsh and Lull, 1907: 98) provided a correct interpretation of the material: "They appear to me rather as representing the superior portion of the occipital, parietal and frontal segments of the skull...." Hatcher disagreed with Lambe's assignment of *Stegoceras* to the Ceratopsia, even doubting dinosaurian affinities at all. Hennig (1915) considered the systematic position of this genus as uncertain, listing it as *incertae sedis* in his order Predentata. The same year as Hennig's work appeared Nopsca (1915) published a paper in which he considered *Stegoceras* as an ankylosaur and referred it to the Acanthopholididae. Shortly afterward (1917) he published a slightly modified classification in which *Stegoceras* is referred to the subfamily Acanthopholididae [sic] within the family Acanthopholidae [sic]. This assignment is also found in his 1918 paper; in the latter publication, he referred the tooth of *Palaeoscincus asper* Lambe 1902 (probably belonging to an ankylosaur) to *Stegoceras* (as "*Palaeoscincus rugosus*").

Lambe (1918) described additional material of *Stegoceras*, including a well-preserved skull roof with part of the occipital region (now NMC 138) and also an isolated frontoparietal; the latter specimen was referred to a new species, *Stegoceras brevis*. Lambe (1918: 35) erected a new family, Psalisauridae, for the reception of *Stegoceras* and "provisionally" placed it in the Stegosauria (which also included the ankylosaurs in Lambe's usage of [illegible] name). Nopsca (1923) contended that the "Palisauridae" [sic] of Lambe was identical with his Acanthopholididae, continuing the association of *Stegoceras* with the Ankylosauria.

A very important contribution to understanding of the real affinities of the dome-headed dinosaurs was Gilmore's (1924) account of a well preserved skull and postcranial material of *Stegoceras*. This specimen had been discovered by G. F. Sternberg in 1921 and purchased by The University of Alberta. Unfortunately, Gilmore's paper caused considerable confusion as Gilmore considered *Stegoceras* as a junior synonym of *Troodon*. He claimed that the premaxillary teeth of the skull of *Stegoceras validus* were structurally identical with a small tooth from the Judith River Formation of Montana described by

Leidy (1856: 72) as *Troodon formosus* and concluded that the specimens were congeneric. Furthermore, Gilmore pointed out that Lambe's Psalisauridae was not proposed in agreement with the rules of the International Code of Zoological Nomenclature and suggested Troodontidae as a substitute name. The Troodontidae were referred to the "orthopodous dinosaurs". Gilmore's taxonomic procedure was followed by most authors until the 1950's. In fact, Nopsca (1901) had already recognized that *Troodon formosus* was based on the tooth of a small theropod dinosaur (see Sues (in press)).

Other workers (Gregory (in Osborn 1924: 10) and Romer (1927: 228)) placed *"Troodon"* in the Ankylosauria but the reasons for such an assignment were inadequate or not presented at all. Nopsca (1929 and 1931) rejected Gilmore's views and contended that Gilmore's specimen actually was a composite, consisting of an ankylosaur skull, the postcranial remains of an (otherwise unknown) ornithopod and some fish bones. Gilmore (1931) and Russell (1932) thoroughly examined Nopsca's comments and rejected his interpretation. In the period from 1924 to 1943, there was but little addition to the knowledge of dome-headed dinosaurs. Sternberg (1926: 104) listed *"Troodon* sp.*"* from the Edmonton Formation of Alberta. Gilmore (1931) described a large frontoparietal from the Lance Formation of Wyoming as *Troodon wyomingensis;* in 1936, he referred a second specimen to this species.

A very detailed monograph on all specimens of "troodont" dinosaurs then known was published by Brown and Schlaikjer in 1943, describing two new species of *"Troodon"* (*T. sternbergi* and *T.*

edmontonensis) and a new genus, *Pachycephalosaurus*, with two new species *(P. grangeri* and *P. reinheimeri)*. *Troodon wyomingensis* was referred to *Pachycephalosaurus* and considered to be a third species of that genus. Brown and Schlaikjer discussed the affinities of the dome-headed dinosaurs and placed them in the Ornithopoda, rejecting ankylosaurian affinities on the basis of the interpretation "that nearly all the nodosaur resemblances they possess are superficial" (Brown and Schlaikjer 1943: 146).

Sternberg (1945) reconsidered the classification of the "troodont" dinosaurs. He demonstrated that *Stegoceras* could not be considered as a junior synonym of *Troodon*, which he correctly recognized as a small theropod dinosaur. Sternberg (1945: 535) proposed the very descriptive new name Pachycephalosauridae for the family represented by *Pachycephalosaurus* and *Stegoceras*. Furthermore, he described yet another species, *Stegoceras lambei*, from the Judith River Formation of Alberta. During the period from 1945 to 1971 there is but a single published addition to our knowledge of the Pachycephalosauridae: the first record of this family from East Asia. Bohlin (1953: 32 - 33) described an incomplete frontoparietal from the Upper Cretaceous of Tsondolein-Khuduk, Kansu, China, as *Troodon bexelli*. The specimen differs from *Stegoceras* in the few features still recognizable and the exact stratigraphic position of the type locality is unknown.

During the past five years considerable progress has been made in the study of dome-headed dinosaurs. Galton (1971) described a new genus and species, *Yaverlandia bitholus*, based on a small frontal region from the Wealden of the Isle of Wight. *Yaverlandia* is the most primitive pachycephalosaurid yet known, showing a dome-like thickening of each frontal. Furthermore, Galton discussed the significance of the dome in the Pachycephalosauridae and suggested (also in 1970 (1970a) in a semi-popular article) that the thickened skull roof served as a battering ram for intraspecific combat. [Colbert (1955: 195) already considered a similar interpretation: "Perhaps (as a very wild surmise) the skull was used as a sort of battering ram."] In 1974, Maryańska and Osmólska published an extremely important monograph on the Mongolian Upper Cretaceous pachycephalosaurids on the basis of specimens collected by the Polish - Mongolian Palaeontological Expeditions to the Gobi desert under leadership of Z. Kielan-Jaworowska. Three new monotypic genera were described; two of them are documented by excellent cranial and postcranial materials, forming the basis for Maryańska and Osmólska's detailed descriptions. A new suborder, Pachycephalosauria, was erected as a taxonomic expression of the morphological uniqueness of these reptiles. *Stenopelix valdensis* von Meyer, 1859, an ornithischian of problematical affinities from the Wealden of N. W. Germany, was also referred to the Pachycephalosauridae. *Stenopelix* is based on a pelvic girdle, a hind-limb and some vertebrae; the original was recently rediscovered (Schmidt 1969). Maryańska and Osmólska's work provides valuable data for determining the contents and affinities of the dome-headed dinosaurs.

2. Scope of the present study

In comparison with the Mongolian Pachycephalosauridae, the present state of knowledge for the North American species is very inadequate (as Galton (1971) and Maryańska and Osmólska (1974) have pointed out). Most of the species are only documented by isolated frontoparietals and are certainly synonyms of two or three species (on the basis of published descriptions and illustrations, I would consider only *Pachycephalosaurus wyomingensis* and *Stegoceras validus* as valid taxa (see pp. 152 - 157 for discussion)). Furthermore, Gilmore's description (1924) of the incomplete skeleton of *Stegoceras validus* in the collections of The University of Alberta is inadequate and/or incorrect in many points. Plainly, a revision of all North American pachycephalosaurids is needed. A joint project by P. Dodson (biometrical analysis of frontoparietals), P. M. Galton (taxonomy of *Pachycephalosaurus* and *Stegoceras* and anatomy of *Pachycephalosaurus*) and the author (cranial and postcranial anatomy of *Stegoceras*) was initiated in 1975 to improve the current situation.

The purpose of this paper is three-fold:

1. Detailed description of the cranial and postcranial skeleton of *Stegoceras validus* with an attempt to reconstruct aspects of the non-skeletal anatomy.
2. Discussion of selected functional problems, especially the significance of certain aspects of the cranial morphology.
3. Discussion of the affinities of *Stegoceras*, integrating the data of Maryańska and Osmólska (1974) and those of the present study,

and comments on the systematic position of the family Pachycephalosauridae.

A descriptive morphological section always precedes discussions of selected functional problems. I followed the usage of vertebrate zoology (rather than human anatomy) with regard to spelling, capitalization, etc., of anatomical terms.

MATERIALS

The following specimens of *Stegoceras validus* Lambe, 1902 from the Judith River Formation of Alberta form the basis for the anatomical sections of this study:

1. UA 2: An excellently preserved skull and jaws and an incomplete postcranial skeleton. The right side of the skull has been subjected to *post mortem* deformation. Many of the postcranial elements are incomplete and crushed and have been restored with colored plaster (Gilmore (1924) apparently did not note this fact in all cases and at least some of his measurements should be used with caution). The data for the locality of this specimen are: Sternberg Quarry no. 1 (see Map 969A (Steveville), Geological Survey of Canada), S. E. Steveville, Alberta, in lsd. 31, sect. 27, tp. 21, range 12 west of the Fourth Meridian; elevation 2,189.2 feet (*ca.* 667.2 m). The specimen was found in a cross-bedded sandstone with abundant plant debris. Collector: G. F. Sternberg. Collection date: 1921.

2. NMC 138 (cast: NMC 138A): Well-preserved skull roof having part of the occipital region. According to Brown and Schlaikjer (1943: 124), the data for the locality of this specimen are as follows: "... below the mouth of Berry Creek, Red Deer River, Alberta." Collector: L. M. Lambe.

3. NMC 1108: originally well-preserved frontoparietal of a small individual (see Brown and Schlaikjer 1943: pl. 43, figs. 4 - 5), sectioned for histological purposes (thin-sections catalogued with the remaining fragments). According to Brown and Schlaikjer (1943: 124), this specimen was collected at "Sand Creek, Alberta." Collector: C. H. Sternberg. Collection date: 1915.

For comparative purposes, excellent casts of the skulls of the holotypes of *Prenocephale prenes* and *Homalocephale calathocercos*, both Maryańska and Osmólska, 1974, from the Nemegt Formation of Mongolia, and a number of isolated frontoparietals in the collections of The University of Alberta and the Provincial Museum and Archives of Alberta, both Edmonton, have been used. Some of the specimens of *Hypsilophodon foxii* Huxley, 1869 preserved in the British Museum (Natural History), London (see Galton 1974a), and specimens of *Fabrosaurus australis* Ginsburg, 1964, currently under study by Prof. A. W. Crompton, Harvard University, have been examined by me to clarify certain structural details.

ABBREVIATIONS

Abbreviations used in the illustrations and tables are as follows:

I. Institutions:

NMC - National Museum of Natural Sciences, Ottawa.

UA - Department of Geology, The University of Alberta, Edmonton.

II. Skeleton:

A. Orientation of elements:

ANT - anterior.

DIST - distal.

POST - posterior.

PROX - proximal.

B. Skull and mandible: abbreviations after Romer (1966: fig. 109), with addition of:

f.i. - foramina for the cutaneous branch of the inferior alveolar nerve.

f.q. - quadrate foramen.

f.p. - articular surface for predentary.

so (I,II) - supraorbital (I,II).

APF - anterior palatal opening.

EN - external narial opening.

ITF - infratemporal fenestra.

OR - orbit.

PPF - posterior palatal opening.

STF - supratemporal fenestra.

C. Postcranial skeleton:

AC - acetabulum.

AT - antitrochanter.

CO.F. - coracoid foramen.

DP - deltopectoral crest.

GL - glenoid cavity.

H - head of humerus.

ISH - ischial head.

OL - olecranon process.

PP - pubic peduncle.

S(4,5) - facet for articulation of sacral rib (4,5).

III. Musculature:

AEM - *M. adductor mandibulae externus, pars medialis.*

AEP - *M. adductor mandibulae externus, pars profundus.*

AES - *M. adductor mandibulae externus, pars superficialis.*

AP - *M. adductor mandibulae posterior.*

DM - *M. depressor mandibulae.*

OM - *M. obliquus capitis magnus.*

PcaML - *M. longissimus capitis, pars transversalis capitis.*

PceML - *M. longissimus capitis, pars transversalis cervicis.*

PST - *M. pseudotemporalis.*

PTV - *M. pterygoideus, pars ventralis.*

RA - *M. rectus capitis anterior.*

RP - *M. rectus capitis posterior.*

SP - *M. spinalis capitis.*

IV. Measurements:

Ghc - greatest height of centrum (posterior).

Glc - greatest length of centrum.

Gwc - greatest width of centrum (posterior).

L - length.

M_w - minimum width of shaft.

W_d - distal width of element.

W_p - proximal width of element.

CV - caudal vertebra.

DV - dorsal vertebra.

MCV - mid-caudal vertebra.

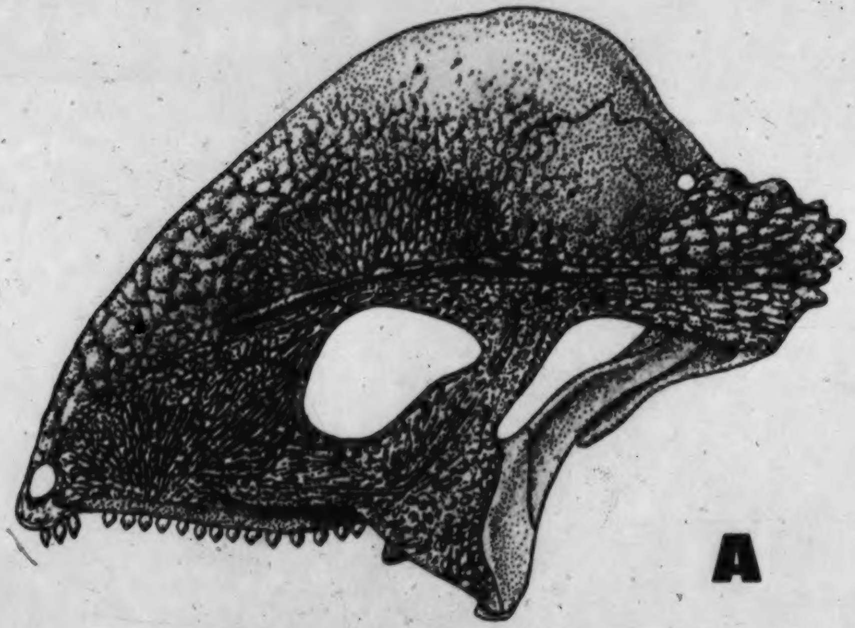
1, 2 - see diagram for Table 2.

PART ONE. CRANIAL SKELETON

1. Skull

The skull of *Stegoceras* (figs. 1 - 4) is subtriangular in lateral view. The snout is foreshortened. A relatively thick shelf is formed by the squamosals and parietals and overhangs the occipital region. The frontals and parietals are greatly thickened, forming an elevated dome. The surface of the dome is relatively smooth and only shows a number of scattered foramina (presumably for blood vessels from the superficial tissues). Much of the external surface of the skull is heavily ornamented with conspicuous nodes. These nodes show a tendency to be arranged in rows, especially along the posterior margin of the parietosquamosal shelf, where the most prominent ones form stout, spine-like structures. The region of the suspensorium is markedly swung forward so that the mandibular articulation lies below the posterior margin of the orbit. Concomitantly, the slit-like infratemporal fenestra slopes anteroventrally. The supratemporal fenestra is extremely reduced (the right fenestra in UA2 even to a higher degree than the left one). The orbit is large, deep and imperfectly elliptical (the longest axis being directed anteroposteriorly); it faces laterally but also slightly anteriorly. The *lamina orbitonasalis* and *planum supraseptale* are well-ossified. The external narial opening is large and situated forward. The occipital region shows a marked anteroventral slope. The occipital condyle is deflected posteroventrally. The basicranium is shortened anteroposteriorly and almost completely

Figure 1. Skull of *Stegoceras validus*, UA 2. Lateral view (slightly restored). X 0.5.



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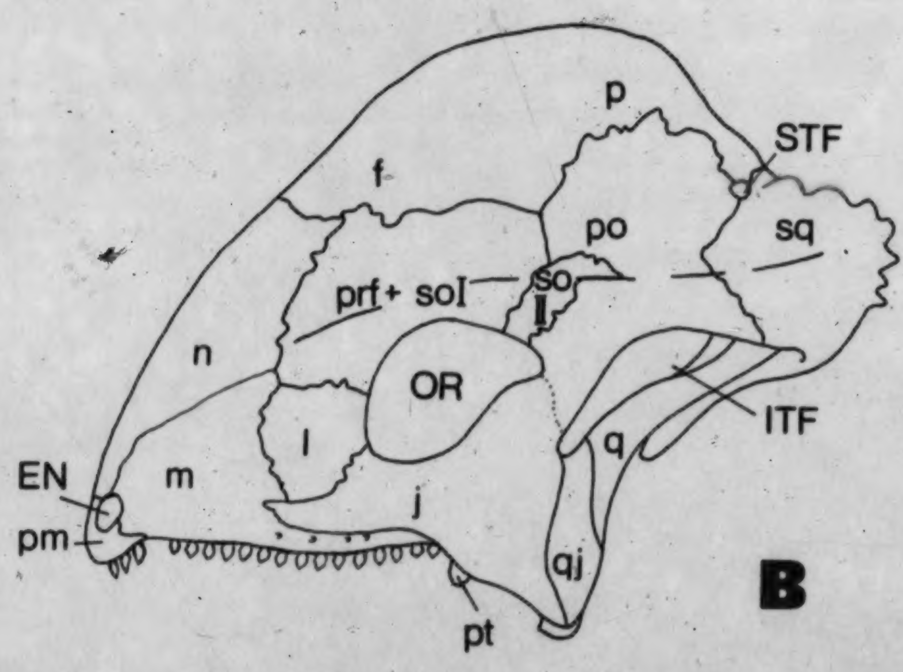

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Figure 2. Skull of *Stegoceras validus*, UA 2. Dorsal view (slightly restored). X 0.5.

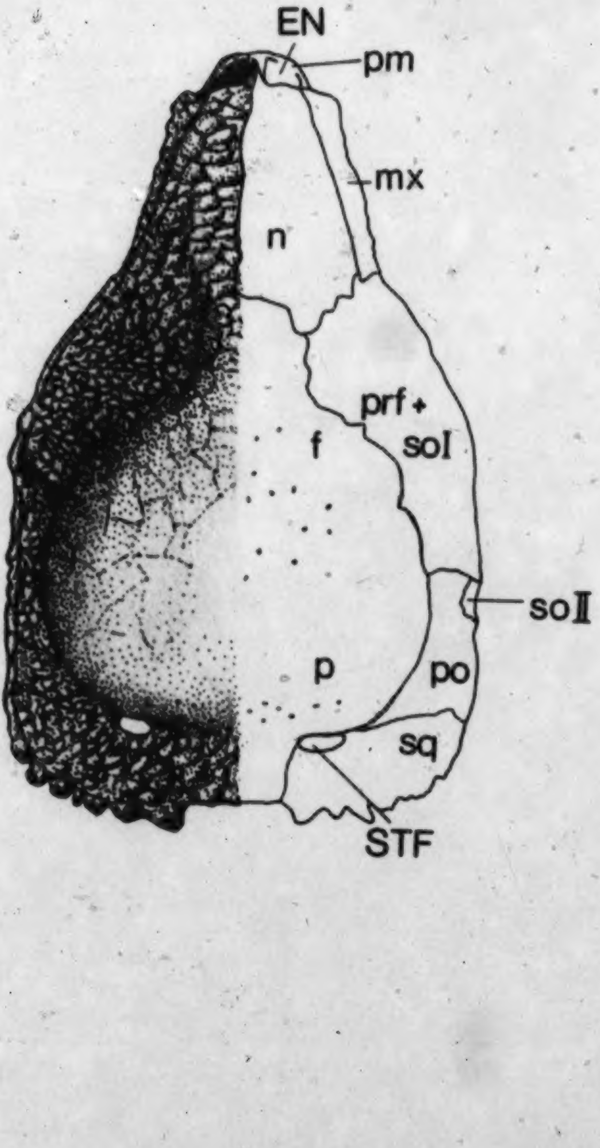
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Figure 3. Skull of *Stegoceras validus*, UA 2. Ventral view (restored). X 0.5.

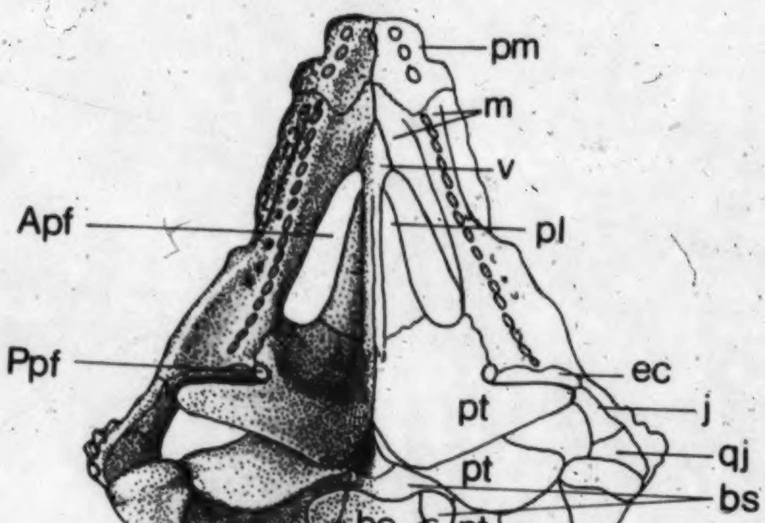
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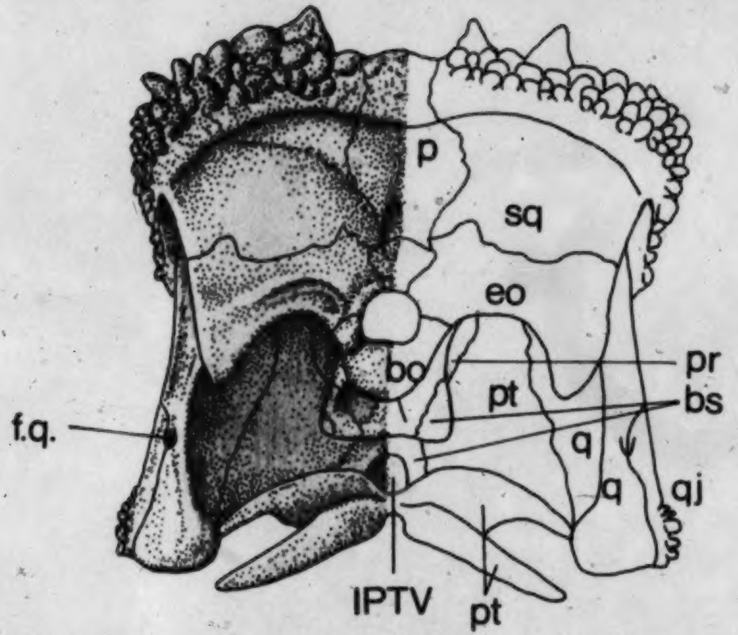
Figure 4. Skull of *Stegoceras validus*, UA 2. Occipital view (restored). X 0.7.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separated from the palatal and suborbital regions by the extension of the pterygoid and quadrate and the juncture of the prootic and basisphenoid with the quadrate wing of the pterygoid.
The dentition is heterodont and consists of comparatively small teeth arranged in a simple marginal row in each jaw. The dental formula is $\frac{\text{pmx. } 3 + \text{mx. } 16}{\text{de. } 17}$.

The descriptions of individual cranial elements are mainly based on the study of the skull of UA 2, with notes on NMC 138 if the latter specimen provides additional information. Detailed comparisons of most cranial elements for most pachycephalosaurid species have been made by Maryańska and Osmólska (1974) and only where my study of the skull of *Stegoceras validus* has produced additional data for comparison, have comments been included.

Premaxilla - The premaxilla is relatively large and has a short posterior process (fig. 1). The body of the bone is low anteriorly. The margin of the premaxilla is thickened and rugose. Three teeth are present and are separated from those of the maxilla by a short diastema. The anterior margin of the premaxilla near the midline of the skull lacks teeth. At the level of the second premaxillary tooth, a small foramen is situated on the suture joining the premaxillae ventrally (fig. 3). It opens into a canal continuing into the narial cavity. This foramen was perhaps connected with Jacobson's organ (although it is uncertain whether this organ was present in archosaurs (Parsons 1959: 20)). An internarial bridge is formed by the dorsal process of each premaxilla. The dorsal margin of the premaxilla is embayed by the external narial opening. The suture joining the maxilla with the premaxilla on the palate is V-shaped. Unlike the condition seen in most ornithopod dinosaurs (and also in *Prenocephale*), the nasal and maxilla are apparently not separated by the posterior process of the premaxilla in *Stegoceras* (see fig. 1).

Maxilla - The maxilla is relatively short but deep. The anterior margin is thick. The sutural contact with the nasal is long. The maxilla meets the jugal posteroventrally and the lacrimal posterodorsally. It participates in the formation of the posterior margin of the external narial opening. Probably an intermaxillary sinus was present (as in *Prenocephale:* Maryańska and Osmólska (1974: 71)); this is indicated by the pattern of crushing of the right maxilla. The lateral surface of the maxilla is convex. Sixteen teeth are present. Above the alveolar margin, the external surface of the maxilla is smooth and is penetrated by a few foramina (probably for nerves and blood vessels) forming a well-defined row parallel to the alveolar margin (fig. 1). The medial part of the maxilla is deep and extends vertically. Near the alveolar margin on the medial side of the maxilla, a number of small foramina (Edmund's (1957) "special foramina") form a distinctive row parallel to the tooth row. The anterior part of the maxilla is relatively wide posterior to the suture with the premaxilla on the palate and meets the corresponding element from the other side of the skull, wedging the vomer in between the maxillae and excluding it from contacting the premaxillae. The entire lateral margin of the anterior palatine fenestra is formed by the maxilla. The maxilla contacts the ectopterygoid posteriorly and the pterygoid posteromedially.

Lacrimal - The lacrimal is a large bone, forming part of the anteroventral margin of the orbit (fig. 1). It meets the anterior process of the jugal ventrally, the prefrontal (including supraorbital I) dorsally and the maxilla anteriorly. The external surface of the lacrimal is ornamented with radiating rows of node-like projections.

Nasal - The nasal is imperfectly quadrangular (fig. 2), thick and heavily ornamented. It joins the maxilla along a relatively straight, long suture (fig. 1), has a relatively short sutural contact with the frontal and an extensive posterolateral contact with the prefrontal-supraorbital I. The suture between the nasals is very long. Anteriorly, a short process underlaps the dorsal process of the premaxilla, contributing to the internarial bridge. The profile of the nasal (see figs. 1 - 2) in transverse and longitudinal direction is convex. The ornament consists of flattened nodes of irregular size and shape.

Prefrontal and supraorbital I - Both bones are fused in *Stegoceras* and are described as a single element in this paper. The element is large and thick, forming much of the dorsal margin of the orbit (fig. 1). Anteriorly, the prefrontal-supraorbital I contacts the lacrimal, posteriorly the supraorbital II and postorbital, and dorsally the frontal and (more anteriorly) the nasal. The external surface is marked by a thin but prominent longitudinal ridge extending just above the orbit, and by numerous nodes.

Supraorbital II - This element forms (together with the prefrontal-supraorbital I) the dorsal margin (figs. 1 - 2) and the roof of the orbit. Its existence was not recognized for a long period of time. Lambe (1918: pl. 1, figs. 1 - 2) noted a small bone posterior to the supraorbital I in NMC 138, which he called "postfrontal". Galton (1971: fig. 4b) gave a line drawing of the same specimen, labelling the same bone "prefrontal". Gilmore (1924) did not recognize this element in UA 2 and thought that the posterodorsal margin of the orbit was only formed by the postorbital and postfrontal (the latter bone is not present in the Ornithischia (Romer 1968)). Maryańska and Osmólska (1974) recognized the presence of a supraorbital II in *Stegoceras* for the first time.

The supraorbital II is a small element wedged between the prefrontal-supraorbital I and the postorbital and forms the posterior part of the orbital roof. Anteriorly, it contacts the supraorbital I, medially the frontal and posteriorly the postorbital. Its external side is heavily ornamented and shows a posterior extension of the thin ridge visible on the prefrontal-supraorbital I.

Postorbital - The postorbital is a large, triradiate bone, forming almost the entire dorsal margin of the infratemporal fenestra (fig. 1) but only a small part of the posterodorsal margin of the orbit. Its dorsal portion is incorporated in the dome (figs. 1 - 2). A ventral process, which is subtriangular in transverse section, meets the dorsal process of the jugal; their sutural contact seems to be directed downward and backward. A posterior process of the postorbital contacts the squamosal; the two bones join along a long suture, forming a massive and wide supratemporal arcade. On the ventral side (visible in NMC 138) the postorbital is underlain by a tongue-like process of the squamosal. Dorsally, the postorbital contacts the frontoparietal, forming the posterolateral part of the dome and participating in the formation of the lateral margin of the supratemporal fenestra. On the ventral side, a stout process with a sharp transverse crest extends medially to meet the laterosphenoid. The crest marks the boundary between the orbit and the infratemporal fossa. The external surface of the postorbital is highly ornamented.

Frontoparietal - As the frontal and parietal cannot be distinguished from each other owing to complete obliteration of any sutures on the dorsal surface of most specimens, they are discussed as a single element in this paper. In some specimens (see, for instance, Galton (1971: fig. 6) and Lambe (1918: unnumbered figure on p. 25)) faint sutures of variable configuration are still visible (see Brown and Schlaikjer 1943). The dome (figs. 1 - 2) is broadly elevated and has a relatively smooth external surface; only the more lateral regions show a markedly rugose sculpture. Anteriorly, the thickened portion of the frontoparietal tapers, forming a narrow bar above and between the orbits. The anterior and posterior margins are trilobed in dorsal view. Anteriorly, the frontal is excluded from participating in the formation of the margin of the orbit by the prefrontal-supraorbital I and the supraorbital II (see fig. 1). Much of the margin of the supratemporal fenestra is formed by the frontoparietal. The reduced size of this opening is the consequence of the thickening of the frontoparietal. Posteriorly, the frontoparietal is narrow and wedged between the squamosals. On the occipital surface, it meets the supraoccipital ventrally and the squamosal laterally and participates in the formation of a large central depression, which is subdivided by a ridge, on the occiput (fig. 3).

Jugal - It is a relatively large and long bone, forming most of the posterolateral margin of the orbit (fig. 1). Its anterior process is very long, extending far forwards and forming a wedge between maxilla and lacrimal. The posterior part of the jugal is expanded vertically and participates in the formation of the anteroventral margin of the infratemporal fenestra. This posterior portion overlaps the quadratojugal along an extensive, nearly vertical suture. The dorsal process of the jugal forms the postorbital bar together with the ventral process of the postorbital. Medially, the jugal contacts a lateral process of the ectopterygoid posterior to the maxilla. The external surface of the jugal shows extensive ornamentation, consisting of a radiating arrangement of ridges and nodes.

Squamosal - The squamosal is a very massive and thick bone. It is not incorporated into the dome (figs. 1 - 2) but is placed laterally to the dome and forms the posterolateral angle of a parieto-squamosal shelf. The posterior margin of the bone is swollen and overhangs the occipital region (figs. 1 - 4). Anteriorly, the squamosal contacts the postorbital dorsally and laterally and overlaps it with a tongue-like process ventrally. Two thin, anteroventrally directed processes embrace the dorsal extremity of the quadrate anteriorly and posteriorly. The posterior process merges into the exoccipital process and is more transversely expanded than the anterior one. The dorsal head of the quadrate fits into a deep cotylus of the squamosal (NMC 138: Lambe (1918: pl. 1, fig. 1) and Galton (1971: fig. 4b)). Medially, the squamosal meets the parietal on the occipital surface, contacting it along an extensive suture, and anteromedially the laterosphenoid. Ventrally, it contacts the exoccipital. A small tongue-like process, wedged between parietal and exoccipital, meets the supraoccipital. The squamosal shows a marked expansion on the occipital surface of the skull. Below the swollen posterior edge of the squamosal a relatively deep, transversely extending and arched depression is visible on the occiput. It invades the parietal medially and ends in the central depression of the occipital surface.

The external surface of the squamosal is heavily ornamented, especially on the thickened posterior and lateral margins. The sculpturing consists of irregular tubercles (see figs. 2 - 3). One well-defined row of spine-like nodes is present along the posterolateral edge, terminating in a prominent, large, pointed tubercle near the sutural contact between parietal and squamosal. A less conspicuous inner row of projections parallels this outer row.

Quadrate - The quadrate consists of a main body formed by a strong and curved shaft and a thin, wide medial lamina overlapping the pterygoid. The long dorsal part of the shaft is inclined posteromedially, while the more ventral portion is nearly vertical to the tooth row (see fig. 1). Only the articular surface for the mandible lies below the level of the tooth row; it is subrectangular and has an almost straight transverse profile. The anterolateral and posteromedial margins of the shaft are well-defined and crest-like.

Quadratojugal - This element is situated between jugal and quadrate. Its ventral margin is but little expanded (in contrast to the condition in *Prenocephale* (personal observation on cast)). The quadratojugal extends posteroventrally close to the mandibular articulation of the quadrate (in lateral view) (see fig. 1). A lateral and a medial lamina can be distinguished but they are less evident than in *Prenocephale* (Maryańska and Osmólska 1974: 73). The lateral lamina is very narrow dorsally but broad ventrally; the situation is reverse for the medial lamina. The quadrate foramen (presumably for the jugular vein) is situated on the suture between quadrate and quadratojugal and opens posteriorly (fig. 4).

Accessory orbital ossifications - A mosaic, formed by small ossifications and surrounded by the frontal, prefrontal (+ supraorbital I), lacrimal, laterosphenoid, orbitosphenoid, presphenoid, basisphenoid and palatine, forms the orbital wall. This region is relatively poorly preserved in UA 2 but with additional study of NMC 138 and extensive comparisons with *Prenocephale* (Maryańska and Osmólska 1974: fig. 3) identification is possible.

A large ossification in approximately the same position as accessory orbital ossification 1 in *Prenocephale* is visible through the left orbit in UA 2. Lambe (1918: pl. 1, figs. 1 - 2 ("Pasp")) labels a small fragment of bone as parasphenoid but this seems to be the upper part of the bone visible in UA 2. This bone may be identified as the homologue of accessory orbital ossification 1 in

Prenocephale. Two foramina (foramina ethmoidala ?) are situated on the posterior suture of this bone. Posteroventrally to this suture, there is another relatively large ossification, which Maryańska and Osmólska (1974: 70) identified as accessory orbital ossification 2. However, this homology is open to discussion as the element under discussion is significantly larger than the supposed homologue in *Prenocephale*.

A third bone, accessory orbital ossification 3 of Maryańska and Osmólska (1974: 70), is clearly visible in UA 2 and NMC 138 (labelled as "presphenoid" by Lambe (1918: pl. 1, fig. 1 ("Psp")) in the latter). It is relatively large, roughly triangular and concave anteroposteriorly. It contacts accessory orbital ossification 1 dorsally above the small opening interpreted as the upper foramen ethmoidale and anteroventrally meets the accessory orbital ossification 2.

Further ossifications are visible on the anterior wall of the orbit in UA 2 but the poor quality of preservation prevents detailed comparison with *Prenocephale*.

Orbitosphenoid - Posterior to accessory orbital ossification 3, a very small bone is visible in NMC 138. It probably represents the orbitosphenoid and is wedged between accessory orbital ossification 3 and the laterosphenoid (= alisphenoid of Lambe (1918) and Gilmore (1924)).

Laterosphenoid - This bone participates in the formation of the upper anterior boundary of the infratemporal fossa (not lower as stated by Gilmore (1924: 21)). The laterosphenoid is not as markedly expanded (dorsoventrally) as in *Prenocephale* (Maryańska and Osmólska 1974: fig. 3).

Parasphenoid - The parasphenoid is probably situated posterior to the interorbital fissure but its dorsal and posterior limits cannot be determined with certainty. As Maryańska and Osmólska (1974: 79) pointed out, the slender pendant process mentioned by Gilmore (1924: 22) in his description of the vomer is probably the ventral extension of the parasphenoidal rostrum.

Basisphenoid - The structure of the basisphenoid is affected by the anteroposterior shortening of the basicranial region (figs. 3 - 4). Posteriorly, the basisphenoid forms the ventrolateral part of the flattened basal tubera, meeting the basioccipital medially and the exoccipital dorsally. The region of the basisphenoid forming the ventral part of the basal tubera is very short vertically. Medially, the basisphenoid is embayed, forming a relatively deep depression. The basipterygoid processes are medially attached to each other and extend anteroventrally, forming the posterior part of the interpterygoidal vacuity. Anteriorly, the basisphenoid probably extends to the posterior margin of the interorbital fissure.

Prootic - This element shows a well-developed external wing extending transversely. The anterodorsal part of this wing defines the medioventral limit of the infratemporal fossa. The ventroposterior part of the external wing underlies the quadrate process of the pterygoid. A crest extends across the latter portion of the prootic, forming the anterodorsal boundary of the middle ear cavity, ventrally continuing towards the basal tubera and contacting the basisphenoid (fig. 3). The prootic is posteriorly overlapped by the basisphenoid. The prootic meets the pterygoid ventrally and laterally and the quadrate laterally and dorsally.

Basioccipital - This element forms the central part of the basal tubera, most of the subreniform occipital condyle and the floor of the medulla oblongata. The junction of the basal tubera is marked by a well-developed keel, flanked by a small depression on each side (figs. 3 - 4). The neck of the occipital condyle is short. The condyle shows a strong ventral inclination, more marked than in any other pachycephalosaurid known so far. Anteriorly, the basioccipital expands slightly and contacts the basisphenoid. Dorsally, the basioccipital meets the exoccipital in the region of the occipital condyle; furthermore, it contacts the exoccipital dorsolaterally outside this region and laterally within the walls of the cavity of the medulla oblongata.

Exoccipital - The exoccipital (fig. 4) participates in the formation of the margin of the foramen magnum. The condylar pedicle shows a small lateral foramen for the exit of the *N. hypoglossus* (XII). The pedicle sends a short process ventrolaterally to participate in the formation of the basal tubera. This process meets the basioccipital medially and the basisphenoid ventrally. The exoccipital forms the wing-like processes ("paroccipital processes" of authors), which are closely attached to the squamosals dorsolaterally. The distal ends of these processes are relatively short. A well-developed, transversely elongated depression, dorsolaterally defined by a ridge extending to the ventral edge of the exoccipital process, is present on the posterior surface of the exoccipital near the ventral margin.

Supraoccipital - The supraoccipital is relatively small and rhomboidal, forming the dorsal margin of the foramen magnum and the roof of the cavity of the medulla oblongata (fig. 4). It is visible in UA 2 and also in NMC 138 (where it was misidentified by Lambe (1918) as an exoccipital). The sutures are partly obliterated. Laterally, the supraoccipital contacts the exoccipital and squamosal and dorsally the parietal. A deeply concave (in vertical direction) central depression, subdivided by a well-developed median ridge into two deep grooves, is present on the supraoccipital.

Opisthotic - Maryańska and Osmólska (1974: 65) note the presence of a small opisthotic in *Stegoceras*, claiming that the sutural contact with the exoccipital "is placed immediately on the ventral margin of the paroccipital process". The quality of preservation in UA 2, however, precludes a determination of the sutures of this element.

Vomer - The vomer is a very long and narrow element, bisecting the anterior palatal opening as a vertical plate (fig. 3). Anteriorly, the vomera are fused into a median bar. The anterior end meets the maxillae at their median contact. Laterally, the medial surfaces of the palatines contact the dorsal margins of the vomer. The posterior part of the vomer is damaged but was probably Y-shaped as in *Prenocephale*. The "pendant process" described by Gilmore (1924) in UA 2 probably represents part of the parasphenoid rather than the posterior part of the vomer (Maryańska and Osmólska 1974).

Palatine - It is a thin, subtriangular bone, tapering anteriorly (fig. 3). The palatine contacts the vomer medially and the pterygoid posteriorly and participates in the formation of the anteroventral wall of the orbit. The anterior process forms part of the margin of the anterior palatal vacuity (internal narial opening), extending almost to the median suture of the maxillae. Posteriorly, the palatine forms the posterior margin of the internal narial opening. The ventral surface of the palatine is markedly arched from its lateral edge medially and dorsally. The posterior part of the palatine, at the sutural contact with the pterygoid, is convex ventrally.

Ectopterygoid - The ectopterygoid is a small, curved element (fig. 3) contacting the posterior and posterolateral part of the maxilla and forming part of the posterior margin of the posterior palatal opening. A relatively stout process of the ectopterygoid meets the jugal. Dorsomedially, the ectopterygoid forms an overlapping contact with the palatal part of the pterygoid; the overlap is not as marked as in *Prenocephale* (Maryańska and Osmólska 1974).

"Epipterygoid" - This element has been described by Maryańska and Osmólska (1974: 78) in the Mongolian pachycephalosaurids but I am unable to verify its presence in UA 2.

Pterygoid - The pterygoid is a large bone with a complex structure (fig. 3). It is shortened (anteroposteriorly) as a correlate of the anterior shift of the occipital region. The pterygoid consists of two almost horizontal and posteriorly inclined processes, a palatal wing and a quadrate wing. Both are relatively thin. The palatal wing shows a slightly inclined, expanded posterior part and a more vertical anterior portion. The vertical part forms the lateral margin of the interpterygoidal vacuity. The posterior extremities of the palatal processes are well separated but more anteriorly a close median contact is established. The dorsal part of the palatal process participates in the formation of the medial wall of the orbit, forming the anterior margin of the interorbital fissure. The quadrate wing is directed dorsally. It can be subdivided into two components: a slightly inclined anterior part and a more extensive, nearly vertical posterior part. The horizontal part contacts the basipterygoid process anteromedially; its posterior margin is free. The medial "joining" of the horizontal portions of the quadrate wings in UA 2 is probably caused by *post mortem* deformation. The vertical part is directed outwards and backwards. Posteriorly, it contacts the pterygoid flange of the quadrate.

2. Lower Jaw

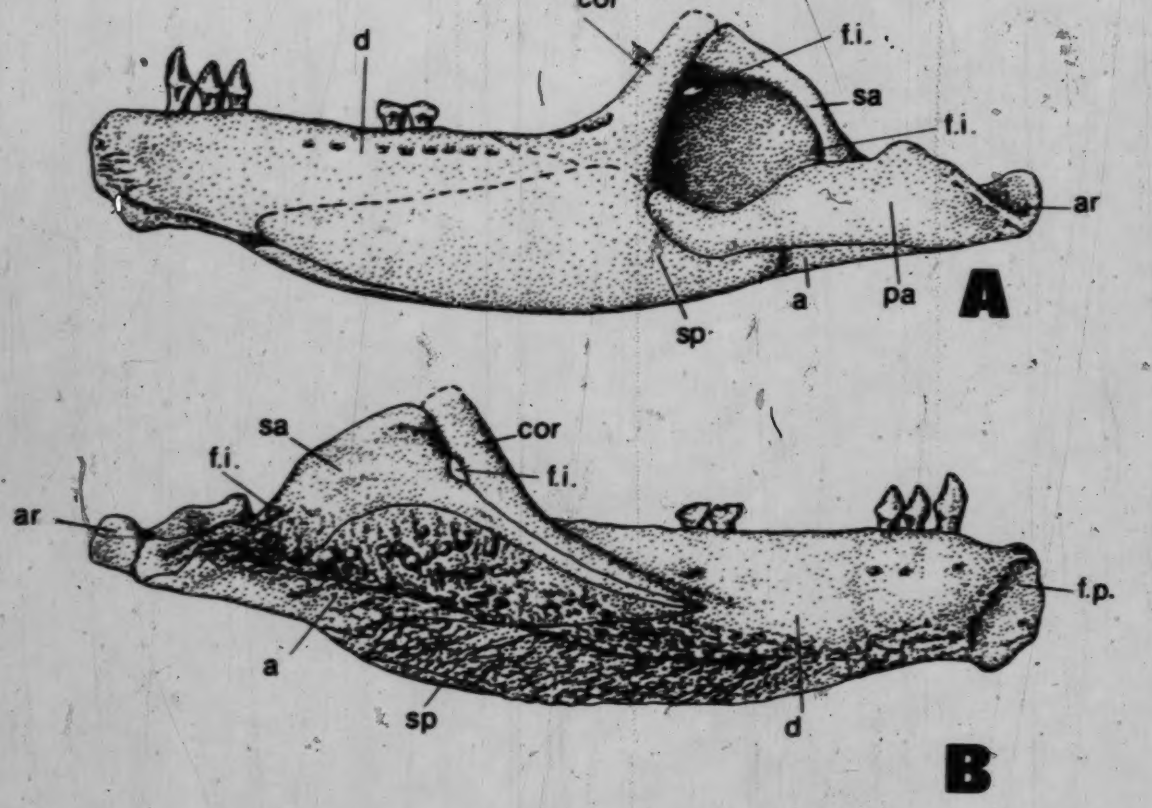
The mandible is well preserved, especially the right ramus (fig. 5). Most of the elements forming the medial side of the left ramus have not been preserved. The right ramus is slightly distorted and its medial side shows numerous fine cracks.

The mandibular rami show a long precoronoidal and relatively short postcoronoidal part. Seven bones participate in the formation of the ramus. The predentary is not preserved but its presence is clearly indicated by surfaces for articulation on the anterior ends of both dentaries (fig. 5, B).

Dentary - The dentary is the largest of the mandibular elements. The symphyseal end is truncated and curves slightly medially, showing well-defined surfaces for articulation with the predentary laterally and medially. The symphyseal connection between the dentaries is weak; they are joined along a slightly obliquely inclined surface. The predentary probably strengthened this articulation. Posteriorly, the dentaries become thicker (with additional thickening occurring lateral to the tooth row) and deeper, reaching their maximum development in front of the coronoid region. The ventral edge of the dentary is rounded except for the symphyseal part where it is sharp. Several large foramina are visible on the lateral surface below the alveolar margin of the right dentary near the anterior end. They probably represent exits of a branch of the *N. trigeminus* (Gilmore 1909: 220) and blood vessels. Ventrally, the dentary underlies the

Figure 5. Right ramus of the mandible of *Stegoceras validus*, UA 2. X 1.2.

(A) Medial view (restored); (B) lateral view.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anterior process of the splenial. Laterally, a pointed process formed by the surangular and coronoid contacts the dentary (fig. 5, B). The dentary shows alveoli for 17 teeth. On the medial side of the left dentary, the Meckelian canal is exposed. It is deep and wide posteriorly but tapers and becomes shallow towards the symphyseal region, ending just behind the symphysis. Most of the Meckelian canal was covered by the splenial. The canal carried the mandibular artery and vein plus the *ramus mandibularis* of the *N. trigeminus* (Romer 1968) and is continuous with the inframandibular fossa. The posterior end of the dentary is embayed by the latter on the medial side. The external side of the dentary bears a rugose ornamentation except for the region below the alveolar margin.

Splenial - The splenial is thin and (in medial view) subtriangular (fig. 5, A). It is slightly exposed laterally (fig. 5, B). The ventral edge appears to be thicker than the other edges and is rounded. The splenial is closely applied to the inner surface of the mandibular ramus and covers most of the Meckelian canal. It meets the prearticular dorsally.

Angular - The angular is the largest bone of the posterior part of the mandibular ramus (fig. 5, B). Its sutural contacts are easily visible on both rami. At its posterior end the angular is overlapped by the articular and surangular and medially by the splenial. Much of the external surface is heavily ornamented. A well-defined longitudinal ridge extends along the external surface.

Surangular - The surangular is relatively large. Its anterior part extends anterodorsally to contact the coronoid. A narrow ventral process underlies a similar process of the coronoid. They parallel each other and extend anteroventrally. Ventrally, the surangular meets the angular along an extensive suture. The dorsal edge of the surangular is thickened and overhangs the inframandibular fossa. Three foramina are visible on the external surface (fig. 5): a large anterior foramen, a smaller posterior one and a small one posteromedial to the latter (not visible in lateral view). They probably represent exits for cutaneous branches of the inferior alveolar nerve (Oelrich 1956) and open into the inframandibular fossa. The posterior part of the surangular is widened horizontally, forming a thin vertical plate on the medial surface of the jaw. The posterior extremity of the surangular is truncated and forms a well-developed lateral boss just in front of the mandibular articulation.

Prearticular and articular - It is not possible to recognize the suture between the two bones in UA 2 and, therefore, they are described as a single element in this paper. Anteriorly, a narrow process of the prearticular forms the ventral margin of the inframandibular fossa and contacts the coronoid, excluding the splenial from the anterior boundary of the fossa. Ventrally, the element meets the splenial and angular and laterally the angular and surangular. The dorsal edge of the element is moderately excavated by the glenoid depression. The posterior extremity of the articular is twisted, being partly turned medially. The posterior end of the retroarticular process curves slightly upward; the dorsal surface of the process is longitudinally and transversely concave.

Coronoid - Although the dorsal extremity of the coronoid is not preserved on both sides of the mandible it probably did not project significantly above the dorsal margin of the surangular. The posterior margin of the coronoid is grooved for reception of the surangular. The distal part of the coronoid is subdivided into two processes: an anteroventrally directed one extending on the medial side of the dentary and a shorter ventral process contacting the prearticular.

Table 1

Measurements of the skull and mandible (in mm)

Greatest length of the skull (= distance anterior extremity of the premaxilla - posterior margin of the parietal (measured on the ventral side))	192
Greatest width of the skull (across the squamosals)	117
Greatest height of the skull	110
Length of orbit	46
Height of orbit	26
Antorbital length of the skull (= distance anterior margin of the orbit - anterior terminus of the premaxilla)	84
Postorbital length of the skull (= distance posterior margin of the orbit - posterior extremity of the squamosal)	73
Length of maxillary tooth row	60
Length of mandibular ramus	140

3. Dentition

Teeth are present on the premaxilla, maxilla and dentary. They are arranged in simple marginal rows and have enamelled crowns. The implantation of the teeth is thecodont. There is no straight cutting edge as the crowns are set obliquely to the long axis of the jaw, slightly overlapping each other from front to back. The dentition is heterodont, the premaxillary and anterior dentary teeth being markedly different from ~~the~~ maxillary and posterior dentary teeth. The maxillary teeth are separated from those of the premaxilla by a narrow diastema (figs. 1 and 3). The teeth correspond to Hotton's type A of dentitions (Hotton 1955: 107) in iguanid lizards, indicating an entirely herbivorous diet (Hotton 1955: 112).

Premaxillary and anterior dentary teeth - There are three premaxillary teeth. The number of teeth in the dentary resembling those of the premaxilla is uncertain but no. 2, 3 and 4 in the right and no. 2 (just erupting) in the left dentary clearly represent this type. The teeth are characterized by taller, more acutely pointed and gently recurved crowns. The anterior and posterior edges of the crowns are ornamented with denticles: eight on the anterior and nine to eleven on the posterior edge. The anterior teeth of the dentary (fig. 5) are larger than those of the premaxilla but are structurally identical.

Maxillary and posterior dentary teeth - The crowns are subtriangular in lingual profile and laterally compressed. The roots are long and show parallel edges. The base of the crown has a cingulum (fig. 6, C). The anterior and posterior edges of the crown are denticulated. The denticles are directed towards the apex of the tooth, compressed and not curved or hooked at their tips. The medial side of the crown is convex vertically and angularly convex anteroposteriorly. It (like the lateral side) is subdivided unequally by a vertical ridge, extending from the base to the apex of the tooth. The external side of the crown is concave vertically and sculptured by a few vertically extending ridges. The number of denticles on the anterior edges is usually slightly larger (one or two more) than on the posterior edges; the average counts for each carina is seven to eight.

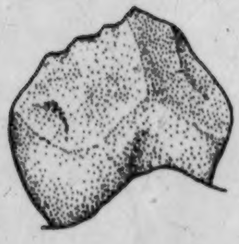
Tooth wear - In a worn maxillary tooth, wear facets are obliquely inclined towards the medial side of the crown and, in a worn dentary tooth, towards the external side, resulting in a downward and outward slope of the occlusal plane. Wear facets are especially well developed on the anteromedial surface of the crowns of the maxillary teeth. Well-defined double wear facets are visible (fig. 6, A-B), very similar to those on the teeth of *Thescelosaurus* (Sternberg 1940: figs. 6 - 7). They are obliquely inclined and perpendicular to each other. Such facets are evidently the result of contact between one maxillary tooth and two dentary teeth. Double wear facets are also known in *Tenontosaurus*, *Camptosaurus* and *Iguanodon* (Galton 1973), *Fabrosaurus* (Thulborn 1971) and apparently even in certain herbivorous lizards, *e.g.*, *Uromastix* (Poole in Thulborn 1971: 170).

Tooth replacement - Edmund (1960: 143 - 144) briefly discussed tooth replacement in *Stegoceras* based on a cast of the skull

Figure 6. *Stegoceras validus*, UA 2.

(A, B) wear facets on two maxillary teeth (in medial view). X 8.

(C) erupting replacement tooth in the left dentary (in medial view). X 2.



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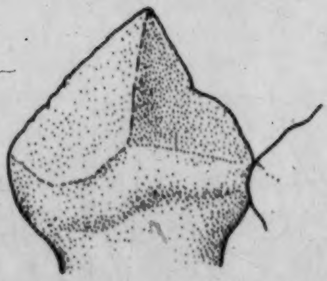

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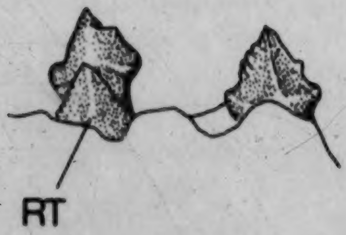


C

of UA 2. A few additional observations from the study of the original permit a reconstruction of the process of replacement.

A row of special foramina (Edmund 1957) is visible on the medial surface of the maxilla, extending subparallel to the alveolar margin (closely resembling the condition in ankylosaurs (see Edmund 1957: fig. 4)). In one foramen (above the alveolus for tooth no. 6) on the right maxilla, a tooth sitting in a crypt lingual to the functional tooth is partly visible. During further development, the crown of a replacement tooth breaks through the medial alveolar wall near the base of an old tooth (no. 11, left maxilla). The replacement teeth are unworn, indicating that growth continued until the level of the occlusal plane was reached. The old tooth probably became loosened and dropped out once the crown of the succeeding tooth had erupted (visible in no. 11 of the left maxilla and no. 12 of the left dentary (fig. 6, C); in the former, the old tooth has already been eliminated).

Edmund correctly compares the type of tooth replacement in *Stegoceras* with that seen in ankylosaurs, stegosaurs and hypsilophodontids. All these groups show a pattern of dental organization corresponding to Edmund's (1960: 136) evolutionary level 1 of ornithischian dentitions.

4. Myology of the head

It is impossible to reconstruct the soft anatomy of fossil organisms with absolute certainty. Many authors have attempted to reconstruct the musculature of certain extinct vertebrates, for only through such work is it possible to approach a reasonable interpretation of certain aspects of the functional anatomy of fossil vertebrates. The first difficulty in such attempts is the determination of the areas of attachment for muscles. Aside from problems owing to inadequate preservation of skeletal material, such work becomes further complicated by the fact that similar locations and even similar functions cannot in themselves establish muscular homologies. During the evolutionary history of a group of organisms, there can be changes in the size and subdivision of muscles, in the position of muscular attachments and even changes in function. The second problem is the correct identification of the muscles. Much confusion has been caused by the application of the terminology used in human and mammalian anatomy, implying correlations with the musculature of these more advanced vertebrates. Recent studies have started to emphasize muscular innervation as the basis for muscular identification as it appears to be relatively conservative and constant for most muscles regardless of changes in function or position.

The attempt has been made in this paper to reconstruct three of the four cranial muscle systems in *Stegoceras:* the mandibular, the axial and the branchial (and hyoidal) system. The orbital muscles cannot be discussed; no impressions of the origins of these small muscles have been observed in *Stegoceras*.

A. Occipital region

The well demarcated occipital region of the skull of *Stegoceras* shows distinct scars of the axial musculature (fig. 7). The influence of these muscles on the shape and topography of the posterior region of the skull is significant and therefore warrants detailed consideration. The terminology used in this discussion follows Nishi (1916), with synonyms used by Oelrich (1956) following in parentheses. Essentially, the pachycephalosaurid axial musculature does not deviate from the typical reptilian pattern, as seen, for instance, in *Sphenodon* and lizards. The discussion of muscle groups follows a subdivision based on function.

a. Extensors

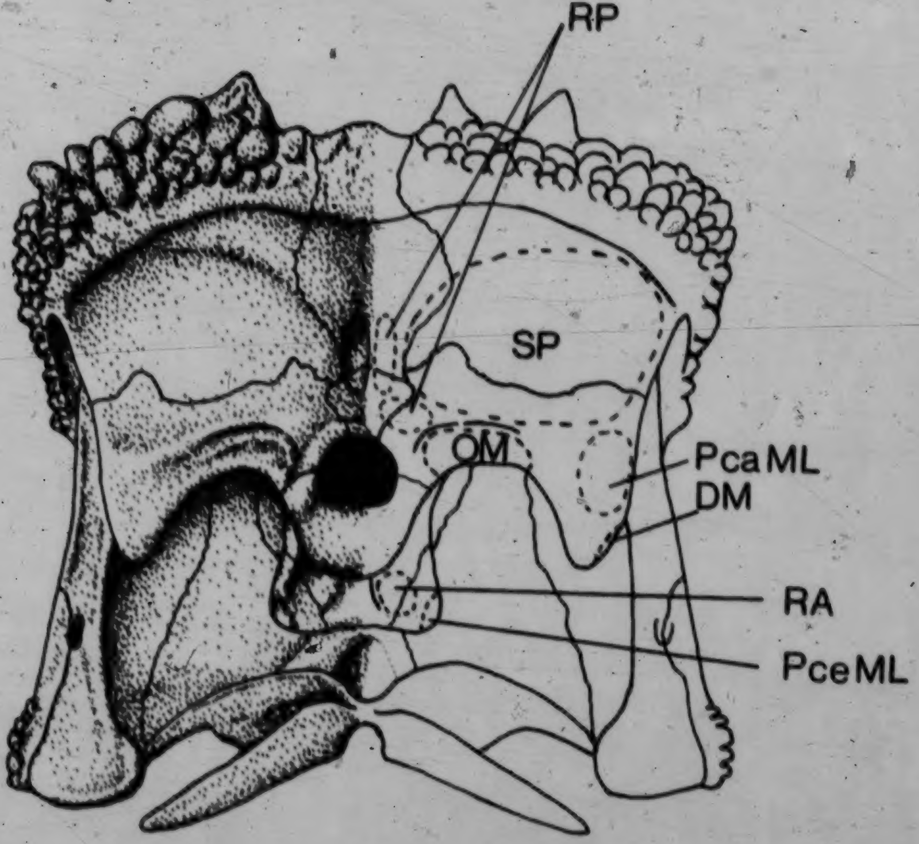
M. spinalis capitis (fig. 7: "SP") - This muscle was probably powerfully developed; a very extensive area of insertion occupies the dorsal part of the occipital region, dorsally being limited by a thick ridge (attachment for *fascia colli superficialis* ?) extending across the squamosal and parietal (as in *Prenocephale* (Maryańska and Osmólska 1974: fig. 6)). Its dorsal position is mandatory if one assumes that its fibers extended caudally to an origin on the neural spines of the posterior cervical and anterior dorsal vertebrae, as in modern reptiles (Ostrom 1961), permitting unrestricted passage for the shorter occipital muscles linking the occiput with the atlas-axis complex. A median vertical ridge probably represents the attachment for the *ligamentum nuchae*. On both sides of this ridge deep pits are visible (as in *Prenocephale* (Maryańska and Osmólska 1974: 95)), probably also functioning as attachment areas for the ligament.

M. rectus capitis posterior (fig. 7: "RP") - This muscle belongs to the suboccipital muscle system whose primary function is support of the head but which is also concerned with abduction, extension and rotation of the head. As in *Prenocephale* (Maryańska and Osmólska 1974) it seems to have two sites for insertion: an area on the exoccipital immediately dorsal to the foramen magnum and the ventral part of the central occipital depression. This may indicate that this muscle was separated into a *pars profundus* and a *pars superficialis* (as in modern reptiles (*e.g.*, *Sphenodon* and *Ctenosaura*; see Ostrom (1961: fig. 55)). This muscle was apparently undivided in hadrosaurs (Ostrom 1961: 115 and fig. 53).

M. obliquus capitis magnus (fig. 7: "OM") - A well-defined area for insertion on the exoccipital, dorsolaterally limited by an arcuate ridge, can be assigned to this muscle. In most reptiles the *M. obliquus capitis magnus* is the largest of the abductor muscles (responsible for lateral deflection of the head) (Ostrom 1961: 116) and typically connects skull and atlas-axis complex.

M. longissimus capitis, pars transversalis capitis (fig. 7: "PcaML") - The area for insertion of this muscle is separated from that of the *M. obliquus capitis magnus* by the ridge mentioned in description of the latter. The *M. longissimus capitis, pars transversalis capitis* (= *M. longissimus cervicis*, Oelrich 1956) functions as a rotator and abductor of the head and, thus (as in *Sphenodon* and lizards), its cranial attachment has to be located far lateral to the midline. As in *Sphenodon* and *Ctenosaura* (Ostrom 1961: fig. 55), its insertion site was probably situated near the lateral extremity of the paroccipital process and close to that of the *M. obliquus capitis magnus*, a

Figure 7. *Stegoceras validus*, UA 2. Skull in occipital view, with inferred areas of muscle attachment (broken outlines).



5

functionally related muscle.

b. Flexors

As in *Prenocephale*, the areas for insertion of these muscles are small and occupy a position close to the midline of the skull.

M. longissimus capitis, pars transversalis cervicis (= *M. longissimus capitis*, Oelrich 1956) (fig. 7: ""PceML") - The area for insertion is placed on the posterior surface of the plate-like basal tubera.

M. rectus capitis anterior (fig. 7: "RA") - The area for insertion for this muscle is medial to that of the *M. longissimus capitis, pars transversalis cervicis*.

The lateral edge of the prootic-basisphenoid plate near its contact with the pterygoid displays depressions similar to those reported by Maryańska and Osmólska (1974: 95) in *Prenocephale*. These scars might have been produced by muscles of the *M. ilio-costalis* system, a lateral muscle system connecting the lateral surfaces of the ribs and the pelvis (Romer 1970). It generally shows a cervical extension connecting the cervical ribs and the atlas-axis complex with the basioccipital.

B. Mandibular musculature

The areas for attachment of the mandibular adductors can easily be determined as most of them are well-defined on the skull of *Stegoceras*. They are generally more posteriorly placed relative to their insertions on the mandible than in other ornithischians - a consequence of the peculiar form of the pachycephalosaurid skull. A similar posterior shift has only been noted in *Protoceratops* (Haas 1955). Ostrom (1961) follows Luther (1914) and Lakjer (1926) in using a tripartite division of the mandibular musculature based on function and innervation:

(1.) *Adductor mandibulae* group.
 Function: closure of jaws.

(2.) *Constrictor dorsalis* group.
 Function: elevation of the maxillary segment (only in forms with kinetic skulls).

(3.) Intermandibular muscles.
 Function: swallowing and breathing.

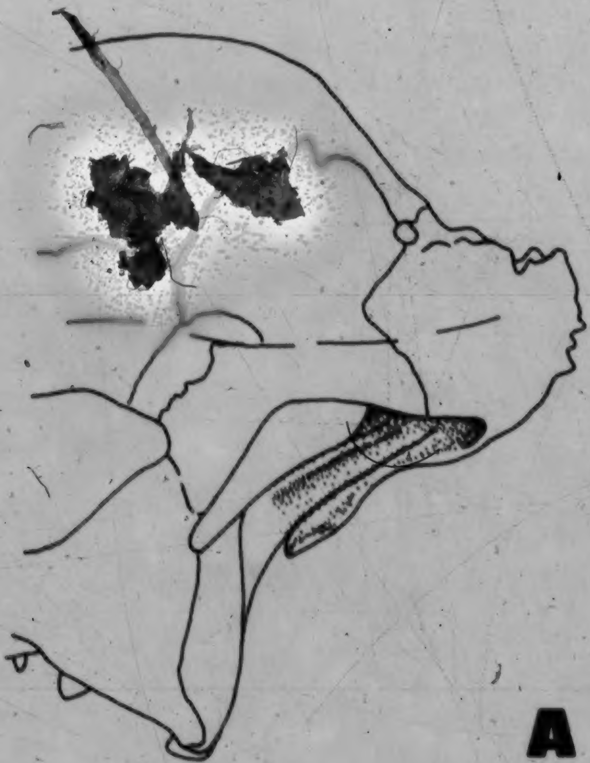
a. *Adductor mandibulae* group

Luther (1914: 44) divides the adductor musculature into external, internal and posterior masses on the basis of their relationships with the three branches of the trigeminal nerve (V).

I. *M. adductor mandibulae externus.*

This muscle occupies a superficial position in the temporal region, lateral to the second (*ramus maxillaris*) and third (*ramus mandibularis*) branch of the *N. trigeminus*. This muscle is typically divided into three parts: *pars superficialis*, *pars medialis* and *pars profundus*.

Figure 8. *Stegoceras validus*, UA 2. Skull in lateral view, showing inferred areas of origin for the *pars superficialis* of the *N. adductor mandibulae externus* and for the *N. depressor mandibulae* (broken outlines).



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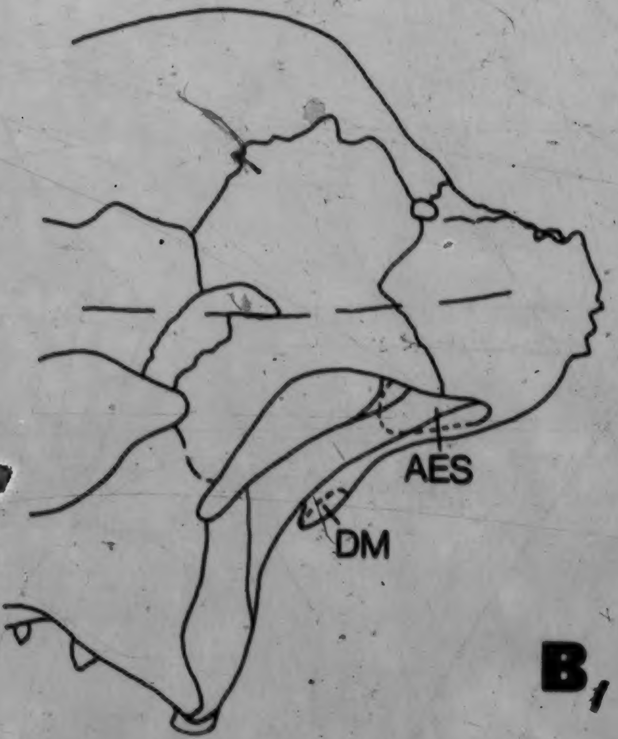


B1

Ia. *Pars superficialis* (figs. 8-10: "AES") - The area of origin is situated on the lateral surface of the squamosal, immediately anterior and dorsal to the head of the quadrate, in a well-defined position. This position is similar to that seen in *Hypsilophodon* (Galton 1974a: fig. 60B) and *Corythosaurus* (Ostrom 1961: fig. 34) but different from the typical reptilian arrangement, where the origin is situated on the medial surface of the upper temporal arch. Perhaps some fibers also extended to a more medial position in *Stegoceras*. The area of insertion can be determined after comparison with *Ctenosaura* and *Sphenodon* (Ostrom 1961: fig. 52) and *Thescelosaurus* (Galton 1973: fig. 7 (= Galton 1974b: fig. 1I)). It was probably situated on the posterodorsal edge of the surangular, between the coronoid process and the glenoid cavity. As this area is relatively wide, perhaps all three parts of the *M. adductor mandibulae externus* inserted here in one common insertion. The existence of a more lateral subdivision of the *pars superficialis*, a *M. levator anguli oris*, on the ventral border of the jugal cannot be verified.

Ib. *Pars medialis* (figs. 9-10: "AEM") - This muscle is situated medial to the *pars superficialis*. It probably occupied a similar position as in hadrosaurs (Ostrom 1961: fig. 36), originating within the infratemporal fossa. It was probably separated from the attachment of the *pars superficialis* by a ridge on the prequadratic process of the squamosal (visible in NMC 138).

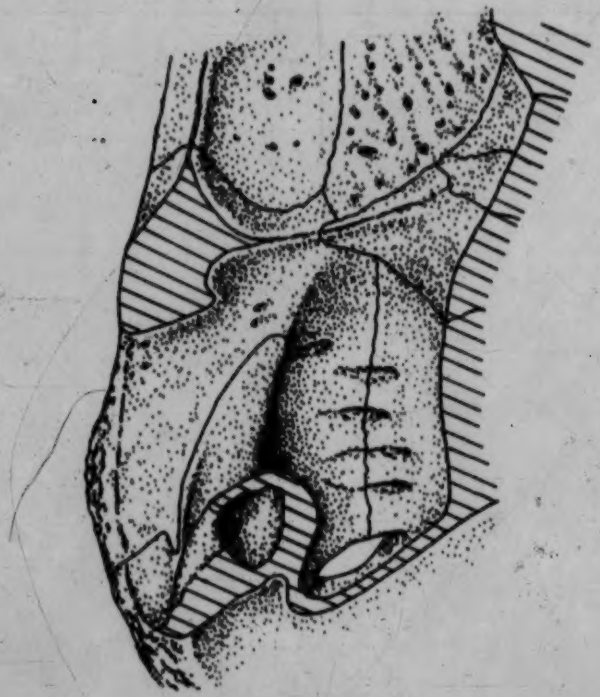
Ic. *Pars profundus* (figs. 9-10: "AEP") - This deepest part of *M. adductor mandibulae externus* fills much of the upper temporal fenestra in modern sauropsids. The supratemporal fenestrae in *Stegoceras* are very small and the *pars profundus* was probably small. Presumably it partly originated on the parietal and partly on the squamosal, below the posterior margin of the supratemporal fenestra. Ostrom (1961: fig. 38) locates the origin of the *pars profundus* in hadrosaurs chiefly on the parietal and squamosal next to that of the *pars medialis*. In *Hypsilophodon*, the *pars profundus* probably originated from the lateral wing and ventromedial part of the parietal and from the medial process of the squamosal (Galton 1974a: 111).

II. *M. adductor mandibulae internus.*

Luther (1914: 57) separates this muscle group into two muscles, the *M. pseudotemporalis* and the *M. pterygoideus* (an unfortunate designation, implying homology with the *M. pterygoideus* in mammals; therefore often designated as the *M. pterygomandibularis* (Hoffmann 1890)). Both muscles occupy positions anterior or medial to the *ramus maxillaris* (V_2) of the *N. trigeminus* and lateral to the *ramus profundus* (V_1) of this nerve.

IIa. *M. pseudotemporalis* (figs. 9, 10, 11, B: "PST") - In modern reptiles, the *M. pseudotemporalis* has its origin from a deep position in the anterior part of the upper temporal fenestra, passing anterior to the trigeminal foramen. In *Hypsilophodon*, this muscle overlapped the *M. adductor mandibulae externus profundus* dorsally, originating from the median crest (Galton 1974a: fig. 60A).

Figure 9. *Stegoceras validus*. Skull roof in ventral view (based on NMC 138), showing inferred areas of origin (broken outlines) for the three divisions of the *M. adductor mandibulae externus*, *M. pseudotemporalis* and *M. spinalis capitis*.



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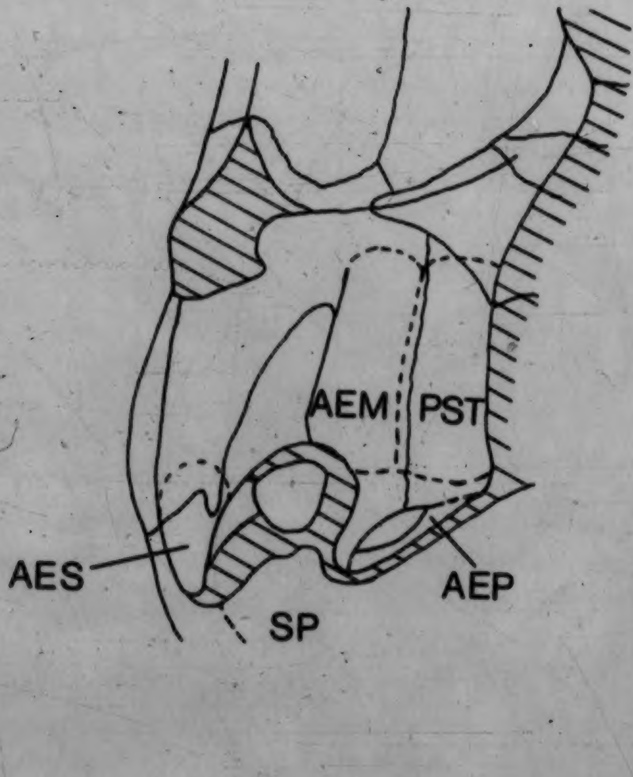

B

Figure 10. *Stegoceras validus*, UA 2. Posterior part of the right mandibular ramus in lateral view, showing inferred areas of insertion of the jaw musculature (broken outlines).

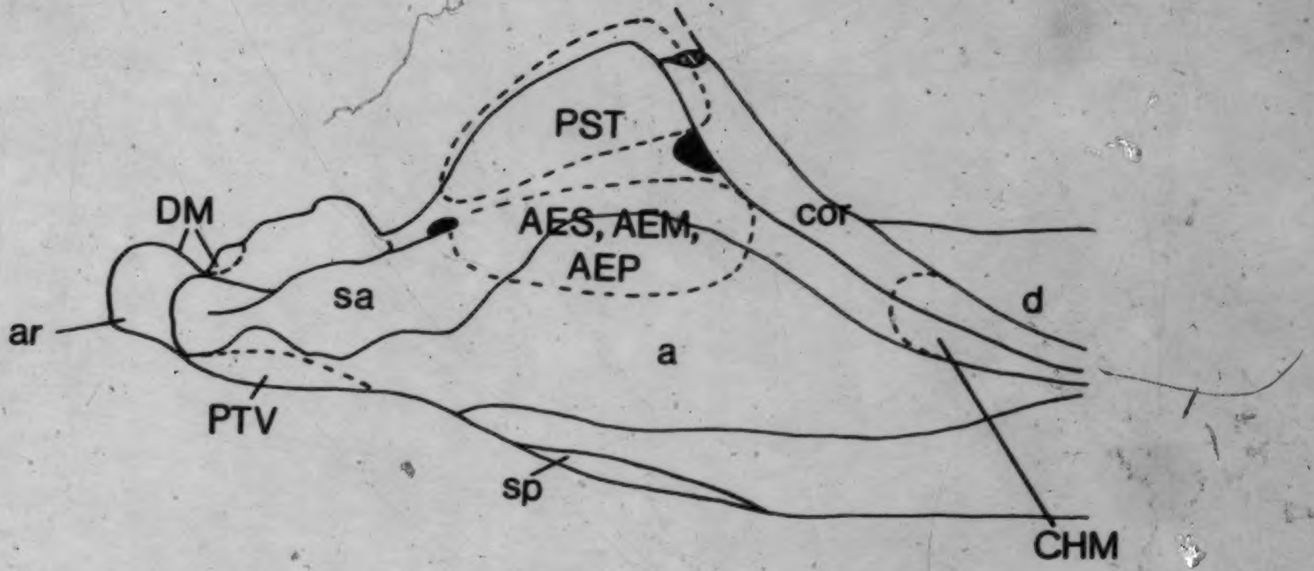
PST
DM
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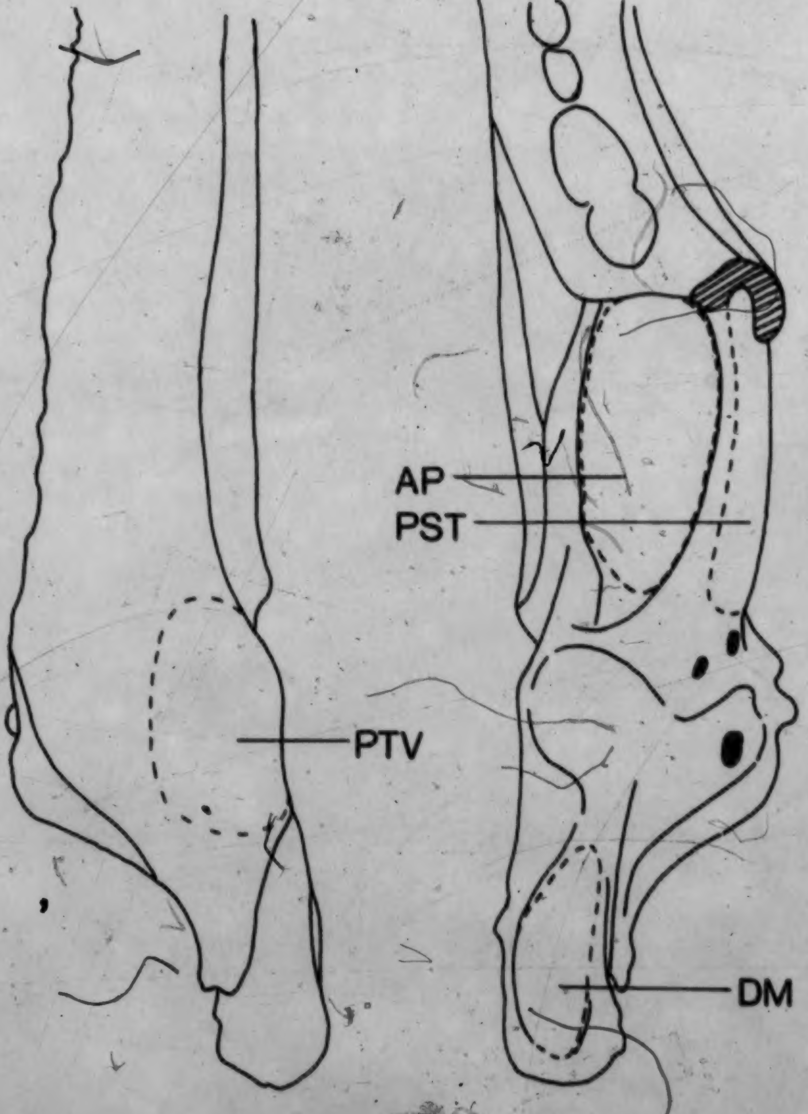
Figure 11. *Stegoceras validus*, UA 2. As Fig. 10; (A) ventral view and (B) dorsal view.



A B

The *M. pseudotemporalis* was probably not the largest of the temporal muscles (as it typically is in modern reptiles) as it would have encroached on the orbit otherwise. It originated within the infratemporal fossa, probably on the lateral surface of the parietal and ventral surface of the postorbital. The area of insertion was probably located on the dorsal, medial and lateral surfaces of the coronoid (as in *Hypsilophodon* (Galton 1974a: fig. 10)), as indicated by well-defined lateral and medial scars. Ostrom (1961: fig. 40) assumed a similar position in hadrosaurs although no clearly defined insertion area is visible on the hadrosaurian mandible.

IIb. *M. pterygoideus* (= *M. pterygomandibularis*, Hoffman 1890) - This muscle is divided into two parts (*pars dorsalis* and *pars ventralis)* in modern reptiles. In his discussion of the muscle in hadrosaurs, Ostrom (1961: figs. 42 - 43) placed the origin of the *pars dorsalis* on the well-developed maxillary shelf (formed by the posteromedial part of the maxilla and by the ectopterygoid). In *Stegoceras*, the *pars dorsalis* probably originated from the dorsal surface of the palatal wing of the pterygoid and inserted on the medial surface of the articular posteroventral to the quadrate (as in hadrosaurs (Ostrom 1961: fig. 41C-D)). The *pars ventralis* (fig. 11, A: "PTV") perhaps originated from the dorsal surface of the quadrate wing of the pterygoid. This muscle presumably wrapped around the retroarticular process to insert on the lateral surface of this process. This area of insertion is well visible on the mandible of *Stegoceras;* it is a concave surface extending from the posterior edge of the glenoid depression diagonally forward and downward. Dorsally, it is bordered by a pronounced, laterally projecting, sculptured ridge and ventrally by a convex angulation representing the ventral border of the retroarticular process. The area of insertion closely resembles that of the corresponding muscle in hadrosaurs (*e.g.*, *Corythosaurus* (Ostrom 1961: fig. 41 A-B)) and also in modern reptiles although it differs in occupying a more anterior position. In *Hypsilophodon* (Galton 1974a: 112), the area for insertion of the *pars ventralis* is probably represented by a small depression below the mandibular articulation.

Stegoceras differs from other small ornithopods in lacking antorbital fenestrae. In *Hypsilophodon* (Galton 1974a) and *Dysalotosaurus* (Janensch 1955), a large fossa is present, which opens posteriorly into the ventral part of the orbit. The function of antorbital openings has been the subject of extensive discussions (for recent reviews see Ewer (1965) and Walker (1961)). It has been suggested that the fenestra housed the origin of an anterior part of the *M. pterygoideus*, inserting close to the articulation on the lower jaw and thus effecting rapid movement of the jaw. This could have been useful for cropping (Galton 1974a). If this interpretation is correct, *Stegoceras* would have differed from the Hypsilophodontidae in this aspect of its feeding mechanisms.

III. *M. adductor mandibulae posterior*

Luther (1914) considered this muscle as being distinct from other adductor muscles in being situated medial and posterior to the *ramus mandibularis* (V_3) of the *N. trigeminus* (Luther 1914: 52). The

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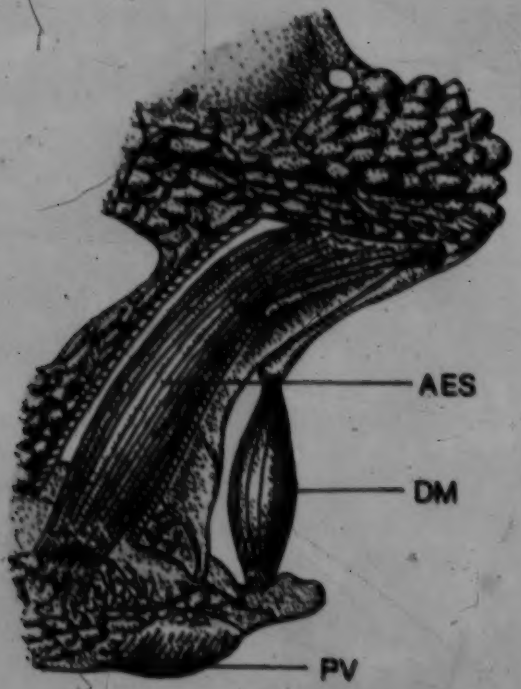
Figure 12. *Stegocer*[illegible]*alidus*. (A) - (C) hypothetical series of dissections, showing the inferred course of the three divisions of the *M. adductor mandibulae externus*, *M. pseudotemporalis* and *M. depressor mandibulae*.



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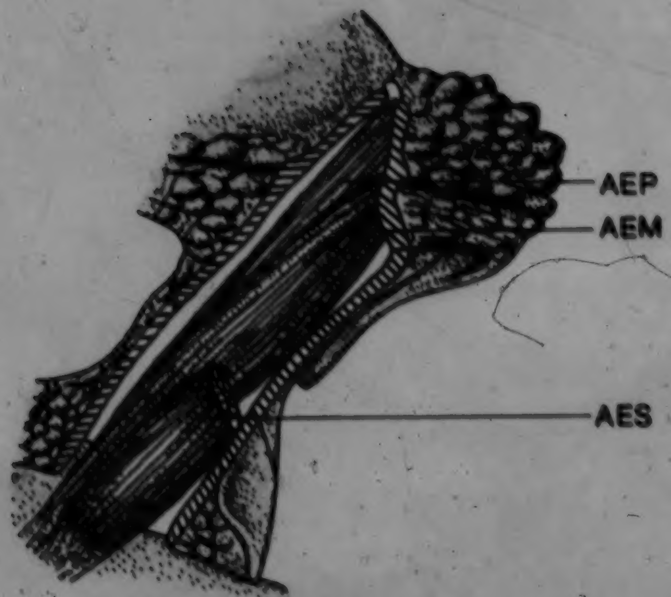

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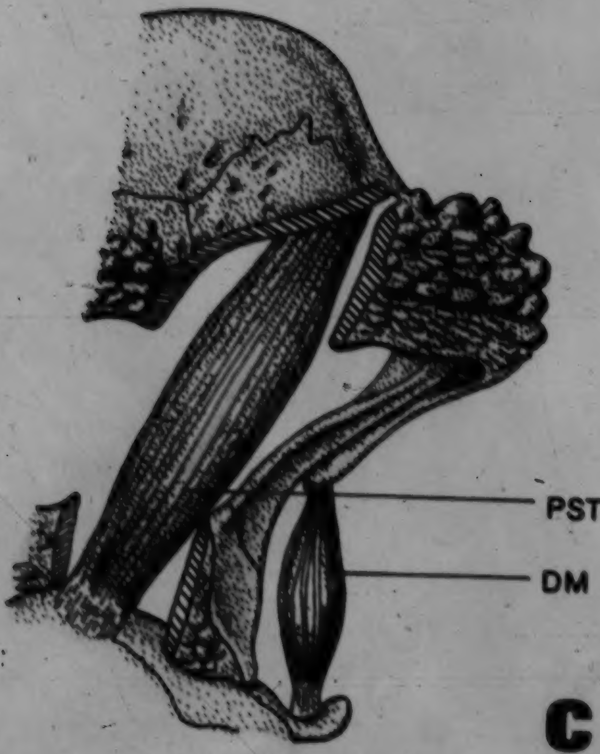

PST
DM
C

M. adductor mandibulae posterior in recent reptiles typically originates from the posteroventral corner of the temporal region, linking the quadrate with the posterior part of the inframandibular fossa. In *Stegoceras*, the area of origin was probably situated on the lower portion of the pterygoid flange of the quadrate on the anterior side and the muscle inserted in the inframandibular fossa. The *M. adductor mandibulae posterior* was probably undivided in *Stegoceras*, as subdivision of this muscle is associated with streptostylic or kinetic conditions of the skull (Ostrom 1961: 106), neither of which existed in *Stegoceras*.

b. *Constrictor dorsalis* group

This group was recognized by Lakjer (1926), who placed the *M. levator bulbi*, *M. levator pterygoidei* and *M. protractor pterygoidei* here. This muscle system is a simplified product of the much more complex system of the more mobile fish skull. Two of the muscles, the *M. levator pterygoidei* and the *M. protractor pterygoidei*, are concerned with the movements of the palatoquadrate (maxillary segment *sensu* DeBeer (1971)) relative to the neurocranial segment. The *M. levator bulbi* is concerned with the movements of the eyelid. Viewing the akinetic nature of the pachycephalosaurid skull, only the *M. levator bulbi* might have been present but an area of origin (presumably on the laterosphenoid as in hadrosaurs (Ostrom 1961: fig. 48)) cannot be recognized.

c. *Constrictor ventralis* group

The muscles of this group are generally thin sheets of fibers extending between the mandibular rami. They are innervated by several branches of the *ramus mandibularis* of the *N. trigeminus*.

M. mylohyoideus - All modern reptiles possess this muscle and therefore it is not unreasonable to infer its presence in fossil reptiles as well. The muscle is a thin superficial sheet (sometimes separated into an anterior and a posterior sheet, *e.g.*, in *Sphenodon* (Fürbringer 1900)) of transverse fibers passing medially to insert in a midline raphe with the fibers from the opposite side. The sheet extends from the symphyseal region back almost to the posterior end of the mandible. Ostrom (1961: fig. 49) believes that an elongate, very gently concave depression on the ventromedial surface of the dentary of *Kritosaurus* may represent the area of origin of the *M. mylohyoideus* but he points out that the evidence for this assumption is insufficient. The presence of a mylohyoid muscle in *Stegoceras* cannot be verified.

d. Branchial musculature

M. depressor mandibulae (figs. 8, 10, 11, B: "DM") - This branchial muscle links the dorsal occipital surface of the skull with the retroarticular process in reptiles. Two sites have been considered as areas of origin for this muscle in *Stegoceras*: the paroccipital process and the posterolateral margin of the squamosal (as has been suggested by Haas (1955) for the Ceratopsia). Given the situation that the latter region was the area of origin, the muscle would have interfered with the tympanum (Haas' proposal was based on the assumption that dinosaurs did not possess a tympanum). It is more likely that the muscle originated on the ventrally deflected paroccipital process, which undoubtedly closely paralleled the direction of the fibers of the depressor muscle. Probably the *M. depressor mandibulae* originated on the ventral extremity of the paroccipital process as has been suggested by Ostrom (1961: fig. 50) for this muscle in hadrosaurs. The retroarticular process in *Stegoceras* is twisted upwards at its posterior end and shows a transversely concave, well-defined dorsal surface posterior to the mandibular articulation. I interpret this site as the area for insertion of the depressor muscle. In hadrosaurs, this muscle probably inserted on the dorsal part of the medial surface of the retroarticular process (Ostrom 1961: fig. 41C).

C. Cheeks

Lull (1908: 694) was the first author to suggest the presence of cheeks in ornithischians. Most authors, however, did not accept this suggestion (see review in Galton (1973)). In 1973, Galton published an extensive discussion of this problem, supporting Lull's ideas of the presence of cheeks. From a functional point of view, cheeks are very important in preventing the loss of food during mastication from the sides of the jaws; in man and mammals, contraction of the *M. buccinatoris* assists the tongue in repositioning the food on the occlusal surfaces of the cheek teeth (Hiiemae and Jenkins 1969:

23). The opponents of Lull's idea (*e.g.*, Brown and Schlaikjer 1940 and Haas 1955) argue that no living sauropsid has cheeks, overlooking the fact that no living sauropsid chews its food. Furthermore, the ornithischian cheek muscle is merely a functional equivalent of the mammalian *M. buccinatoris*.

The maxillary and dentary teeth are inset in *Stegoceras* and a considerable lateral space is formed by the overhanging maxilla and floored by the dentary. The external surface of the maxilla and dentary is smooth for some distance above and below the alveolar margin, respectively. No attachment scars are visible (a fact used in discussions as evidence against cheeks (Ostrom 1961: 102)) but this is not surprising as dissections of mammalian heads reveal practically no evidence concerning the attachment of the *M. buccinatoris* (Galton 1973 and personal observation). The smooth areas on the lower jaw of *Stegoceras* occupy a similar position as those in *Thescelosaurus* (Sternberg 1940: fig. 16; Galton 1973: fig. 7). The cheeks (fig. 10: "CHM") probably extended up to the anterior end of the maxillary tooth row and *Stegoceras* presumably had only a small mouth in a subterminal position, as it has been reconstructed for *Hypsilophodon* (Galton 1974a, fig. 62). Probably the cheek muscle was pinnate (as in many mammals) rather than having vertical fibers (as shown, for instance, by Lull (1908: pl. 1). Pinnation could be advantageous in arranging the muscle in this architecturally unsuitable space (Gans and Bock 1965: 131).

5. Movements of the jaw

Galton (1973: 77) recognized four structural grades of the ornithischian masticatory apparatus. *Stegoceras* can clearly be referred to Galton's grade 2, showing the recessed condition of the maxilla and having obliquely inclined wear facets on the teeth (as in *Hypsilophodon* and most other ornithischians).

The pattern of tooth wear indicates that the jaw action was essentially vertical. A significant anteroposterior movement was probably not possible as certain structural features show:

(1.) the small size of the glenoid surface and its inclination relative to the tooth row (allowing little (if any) retraction);

(2.) the anterior convergence of the tooth rows of the upper and lower jaws (preventing any significant protraction);

(3.) the presence of teeth in the premaxilla and anterior part of the dentary;

(4.) the presence of paired wear facets on the teeth indicating interlocking of the teeth from opposite jaws (effectively limiting protraction and retraction).

Mandibular movement seems to have been restricted to a simple hinge movement about the condyle of the quadrate.

The functional significance of the obliquely inclined wear facets can easily be demonstrated using a parallelogram of forces. A force is applied across two obliquely inclined but parallel surfaces. It can be resolved into two components, one acting parallel to the occlusal surface (= shearing component) and a second perpendicular to the first and perpendicular to the occlusal surface (=crushing component). The degree of inclination of the occlusal surfaces relative to the vertical plane in *Stegoceras* suggests that the shearing component was more important than the crushing component.

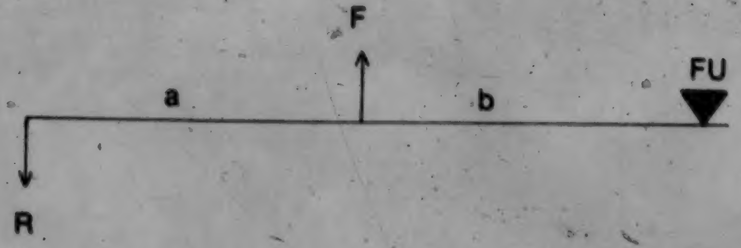
As the dentary teeth presumably were closer together than the maxillary teeth, oblique movement can be postulated with the teeth of only one side in opposition at any given time (as in mammals; Crompton and Hiiemae 1970 and Crompton and Jenkins 1973). Oblique movement of the jaws was possible in *Stegoceras* as the surface for articulation of the articular is smaller than that of the quadrate and only a relatively small amount of shift would have been necessary. The analysis of the possible mode of jaw movement suggests that the action along the occlusal surfaces would have been almost exclusively one of shearing. As the anteromedial wear facets on the maxillary teeth pass forwards at a greater angle than inwards, the jaw movement presumably was not strictly vertical but some pro- and retraction was possible.

An unusual feature of the skull of *Stegoceras* is the complete external covering of the area for the insertion of the main adductors on the mandible; this covering is accomplished by the downward extension of the jugal and quadratojugal and the high position of the surangular. The resulting narrow space for the passage of the adductors indicates that the bulk of these muscles was not very large. The *M. pseudotemporalis* and the *M. adductor mandibulae externus* were probably the main adductor muscles. If the restoration of the jaw musculature is correct, the three divisions of the *M. adductor mandibulae* *externus* had a common line of action and were perhaps more important than the *M. pseudotemporalis*. The forward inclination of the quadrate presumably aided in resisting the forces developed by the main adductors. The lower jaw of *Stegoceras* probably acted as a third class lever (see Davis 1955 and Ostrom 1964) with the applied force acting somewhat obliquely to the mandibular ramus. The well-developed coronoid process and the depression of the glenoid cavity below the level of the tooth row resulted in a lengthening of the moment arms of all the main adductors (relative to the primitive ornithopod condition). This is important as the force, which can be exerted at any point along the tooth row, is not only a function of the magnitude of the applied force but of the moment arm of that force as well. The lower jaw of *Stegoceras* can be considered as a simple third class lever with non-parallel opposing forces (Ostrom 1964): The moment arm of the applied force is distance b, that of the resistant force is a + b if the opposing forces had parallel lines of action (fig. 13, A). In a system with non-parallel opposing forces (fig. 13, B) the amount of available force at any point along the lever will be smaller than in a system with parallel opposing forces as the moment arm of the applied force has been shortened. As b is no longer perpendicular to the direction of the force vector it is no longer the moment arm. A new moment arm perpendicular to the new inclined line of force action, b', results. Its length l is a function of the angle α of inclination of the new force vector:

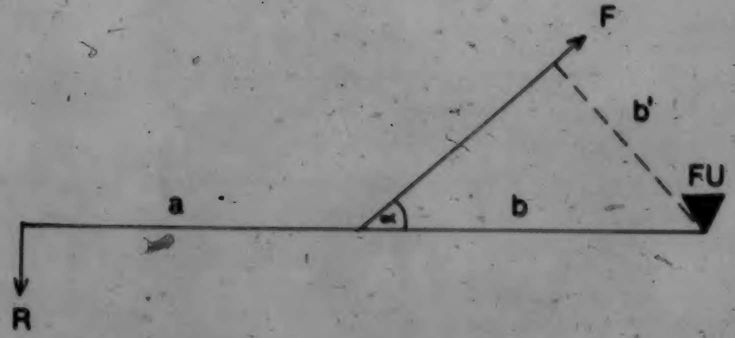
$$l = b \cdot \sin \alpha$$

The critical factor in a mechanical system like the third class lever

Figure 13. Simple third class levers. (A) with parallel opposing forces. Moment arm of applied force equals b. (B) with nonparallel opposing forces. Moment arm of applied force equals b'. Moment arm of resistant force equals a + b in both cases. After Ostrom (1964: fig. 8, redrawn). Symbols: F, applied force; FU, fulcrum; R, resistance; α, angle of inclination for force vector.



A



B

is the length of the moment arm (DeMar and Barghusen 1972); lengthening of the moment arm (*i.e.*, shifting the point of force application away from the jaw joint) increases the effective force acting perpendicular to the jaw ramus.

The *M. adductor mandibulae posterior* only had a small moment arm. Its fibers probably extended parallel to those of the main adductors. It was presumably important during the initial stages of adduction and in preventing (together with the *M. pterygoideus*) disarticulation of the lower jaw. The *M. depressor mandibulae* had but a small moment arm notwithstanding which site of origin is chosen. The functional interpretation of this feature is that the depressor muscle probably had a fast action but exerted little force (which is sufficient as the lower jaw would be depressed by its own weight and little resistance would have occurred).

6. Functional significance of the dome and related structures in the cranial and postcranial skeleton

The pachycephalosaurid skull is unique among the Archosauria in showing an extremely thickened frontoparietal "shield". In *Pachycephalosaurus grangeri*, the largest and most advanced pachycephalosaurid, the frontoparietal of a 624 mm long skull reaches a maximum thickness of 222 mm, producing a bizarre appearance of the skull. This peculiar dome-like structure has been commented upon by many authors since 1902, the date of the description of *Stegoceras validus*. Colbert (1955: 195) was the first author to attempt a functional interpretation of this feature; he suggested

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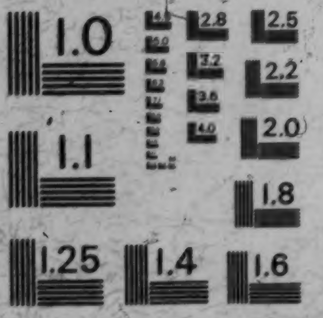

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(as a "very wild surmise") that the thickened skull roof served as a battering ram. More recently, Galton (1971) discussed this possibility more extensively, suggesting that the dome was use for intraspecific competition, and cited anatomical evidence favoring such an interpretation.

In connection with the study of the cranial anatomy, I have attempted to develop a functional model for the explanation of the cranial structure in the Pachycephalosauridae, especially *Stegoceras*. It is the basic assumption of this discussion that the thickening of the frontoparietal *has* an adaptive significance, and is neither nonadaptive nor pathological (as might be suggested). The significant increase (both absolute and relative) in the thickness of the skull roof and the development of related modifications of the cranial structure during the evolution of the Pachycephalosauridae would not have been selected for unless they conferred a selective advantage. There is a possibility that the thickened skull roof acted as a visual display in individual and/or species recognition. I consider this as improbable on the basis of the dense structure of the bone. To my knowledge, purely ornamental functions are accomplished by cancellous bone in all recent vertebrates with cranial excrescences (*e.g.*, *Casuarius*).

The interplay of new techniques with increasing delicacy of the experimental apparatus permits elucidation of very complex functional problems in extant vertebrates. Anatomical inference concerning function can be made from anatomical and behavioral examinations.

However, marked constraints enter into methodology when the attempt is made to decipher the functional significance of the form and structure in fossil vertebrates. Only an indirect assessment can be obtained using analogies with extant taxa that can be studied or using models derived from purely mechanical considerations (like theoretical stress analysis) or actual models approximating real biological situations (experimental stress analysis).

The latter method and mechanical considerations form the basis for the discussion of the mechanical efficiency of certain structural features in the pachycephalosaurid skull for functions predicted from the "butting hypothesis" formulated below. This represents an indirect test of the hypothesis. The method of experimental stress analysis employed in this study utilizes the physical property of photoelasticity. It was chosen because of its visual attractiveness, immediately providing a tangible picture of the mechanical efficiency of the structure under investigation.

Materials and methods - The experimental stress analysis was carried out using the photoelastic methods developed and described by Pauwels (1948) and Kummer (1956, 1959, 1966). A fine plaster cast of the only known skull of *Stegoceras validus* was sectioned in a coronal plane at the level of the highest elevation of the frontoparietal dome and in a sagittal plane. The outlines of the sections were reproduced on 10 mm thick plates of plexiglass and models were cut from these plates with a fretsaw. A slight distortion of the right side of the cranium was not corrected. The edges of the models were manually polished using emery papers of various grain sizes. The *cavum cranii* was reconstructed on the basis of an endocranial cast and estimates from isolated frontoparietals. The models were stressed in polarized light and the isoclines were photographically recorded at each 10° position when the polarizing filters were turned from 0° to 80°. The trajectorial pattern was reproduced by means of Kummer's (1956) photographic method. The load on the model was carefully chosen to obtain clear isoclines without producing any isochromates (which will interfere with the isoclines on the film and make evaluation impossible). The nine pictures of isoclinal patterns were superimposed during development and the resulting print provided an objective reproduction of the trajectorial picture.

Anatomical observations - This section summarizes all relevant data from the preceding sections of the osteology and myology of the head to facilitate the functional analysis.

The frontals and parietals are thickened and fused; their sutures become obliterated. The supraoccipital is fused to the parietal. The *lamina orbitonasalis* and *planum supraseptale* are completely ossified. Laterosphenoid, orbitosphenoid and presphenoid are well-ossified and firmly sutured to adjacent bones. The occiput slopes anteroventrally when the skull is oriented horizontally; corresponding forward inclinations occur in the suspensorium (almost reaching the level of the posterior margin of the orbit), basicranium and infratemporal fenestra. The foramen magnum is reduced in size. The occipital condyle is deflected posteroventrally. The basicranium is

Figure 14. *Stegoceras validus*, NMC 1108. Transverse section through the frontoparietal to show trabecular architecture. X 2.

Vertical section through frontals
near fronto-parietal suture, G.S.C. 1108

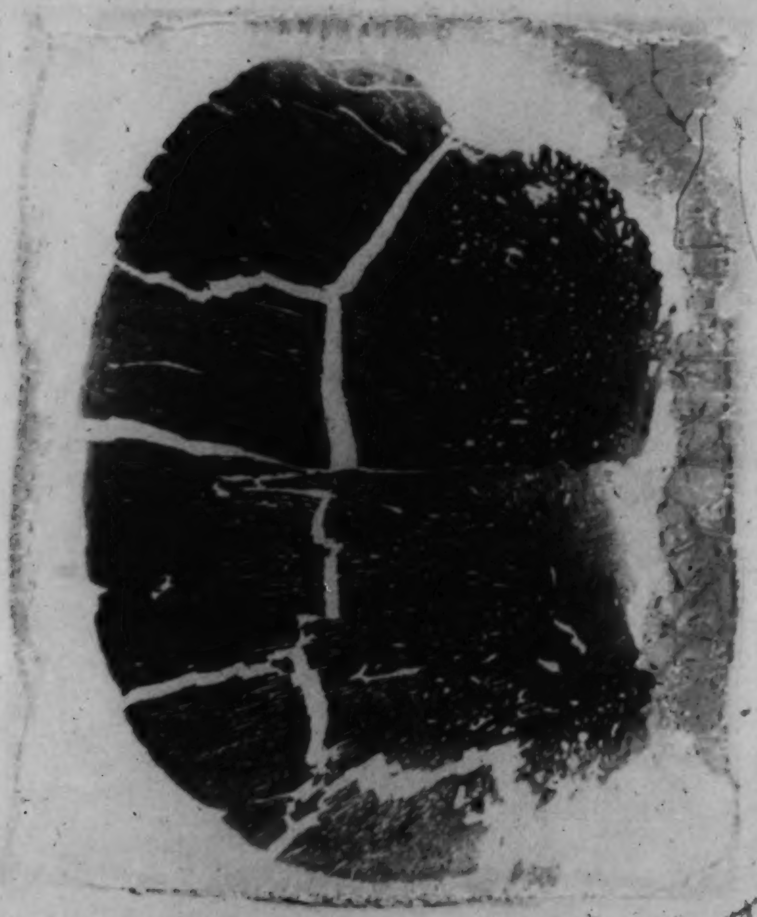


Figure 15. Trajectorial picture of a plexiglas model of a transverse section through the frontoparietal of *Stegoceras*, with load applied in one point.

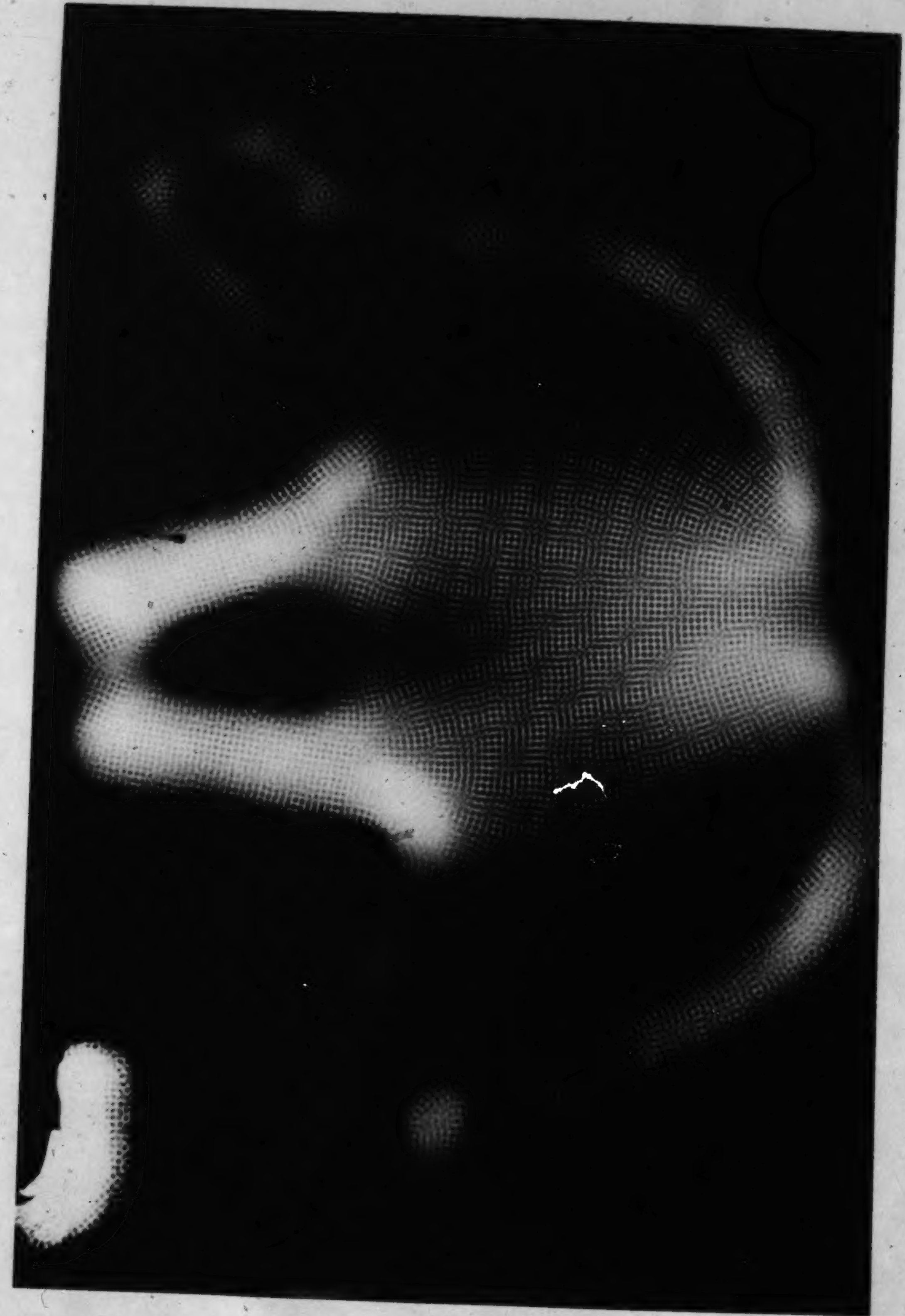


Figure 16. As Fig. 15, with load equally applied to the whole area of possible contact (= trajectorial picture of combined single points).

separated from the palate and suborbital region by the extension of the quadrate and pterygoid and the connection of prootic and basisphenoid with the quadrate wing of the pterygoid. The skull was certainly akinetic.

The nuchal musculature was exceedingly well developed. The extensor muscles, especially the *M. spinalis capitis*, were enlarged, whereas the flexor muscles were relatively small. The nuchal ligament was well-developed.

A significant feature of the postcranial skeleton (see Part Three) is the presence of a tongue-in-groove type of interzygapophyseal articulation in (at least) the more posterior dorsal vertebrae.

Functional analysis - The butting hypothesis states: "The thickened frontoparietal and related modifications of the cranial structure are adaptations to (intraspecific) combat employing pushing and/or ramming with the head." The following predictions concerning structural modifications of the pachycephalosaurid skull can be derived from the butting hypothesis:

(1.) Reorientation of the head on the vertebral column into a position suitable for the reception of impact forces by the skull.

(2.) Creation of a bony architecture and support of the head "shield" structurally suitable to resist such forces.

(3.) Positioning of the occipital condyle to reduce the moment arm of the impact force producing flexion at the atlanto-occipital junction.

(4.) Formation of a suitable area for contact on the dorsal surface of the skull roof.

(1.) *Reorientation of the head* - It is difficult to be certain about the posture of the neck since the cervical vertebrae are not preserved in any of the three incomplete postcranial skeletons of pachycephalosaurids recovered so far. As Galton (1970b) pointed out, the vertebral column of ornithopods was probably held horizontally during running. As the occipital condyle is deflected posteroventrally in pachycephalosaurids, it is very difficult (if not impossible) to articulate it with the atlas if the cranium and atlas-axis are horizontally oriented. This situation can be corrected by three different modifications:

(1.) ventral inclination of the skull (*i.e.,* rostral end lower than occipital end), or

(2.) ascent of the cervical column to articulate with the skull, or

(3.) both.

Probably both of these changes resulted in an angulation between the axes of the cranium and cervical column in pachycephalosaurids, the typical condition in mammals (Jenkins 1971) and different from the majority of living and fossil reptiles, in which the long axis of the cervical column is horizontal with that of the cranium. Then the frontoparietal region would have faced forward (as suggested by the inclination of the occiput and quadrate) if the cervical column was horizontal. Furthermore, the angulation would permit greater freedom in extension and flexion and also provide a longer lever arm for the extensor musculature. Aside from the posteroventral deflection of the occipital condyle, the anterior displacement of the infratemporal fossa and suspensorium seem to provide evidence for a flexure between the axes of the cranium and cervical column. With the decrease in the angle between head and neck the mandibular articulation shifted forward and away from the retromandibular musculature, preventing encroachment of both the mandible and the articulation into the cervical region (Barghusen 1975).

(2.) *Structure of the dome and its supports* - Examination of isolated frontoparietals of *Stegoceras* reveals that they consist of dense bone. The histological picture (fig. 14) shows a radiating arrangement of numerous small trabeculae in a dorsal zone and a more vascularized ventral zone where the trabeculae merge. No clear differentiation between spongiosa and compacta exists. The thickening of the bones is the result of upgrowth of the trabeculae and not of fusion of dermal ectopic elements with the underlying frontal and parietal. The histological characterization suggests classification of this type of bone growth as a diffuse form of classical pachyostosis *sensu* Kaiser (1960). Galton (1971: 45) suggested that the arrangement of the trabeculae "is ideal for resisting a force applied against the top of the dome"; however, no further discussion was included. The radiating pattern of the trabeculae and the fact that the trabeculae are oriented in a perpendicular fashion to the surface of the frontoparietal invite a functional explanation. Working with the trajectorial theory of bone architecture, the trabeculae could be considered to be compressive resistant (Evans (1957: 198)).

In the first experiment of the photoelastic study with a model of a coronal section, a force was applied to the highest point of the dome. [During the experiments the location of the support of the models was somewhat oversimplified as the atlanto - occipital junction is not precisely located below the highest point of the dome; but this is not relevant in the present context as the experiment is restricted to two-dimensional patterns of trajectories.] The resulting trajectorial picture (fig. 15) did not show any resemblance to the histological picture. This is hardly surprising as it is extremely unlikely that impacts will always occur at the same point. In the second experiment, equal forces were applied to several points of the possible area for frontal contact. [For experimental purposes (and taking into account a slight distortion of the cranium) a support of the whole area of possible contact proved to be more satisfactory than support of individual points and subsequent combination of the resulting pictures of trajectories.] The resulting pattern of trajectories (fig. 16) is an excellent approximation of the bony architecture (as revealed by the histological examination). The forces are transmitted through the lateral walls of the braincase; this suggests that the unusually well ossified braincase of *Stegoceras* was the main structural support of the frontoparietal "shield".

Summarizing, it can be safely concluded that the trabecular architecture of the frontoparietal is in fact suitable for force transmission and that the unusually well ossified braincase can also be explained in such functional terms. Although compact bone has much larger compressive strength than spongy bone, spongy bone is more suitable for energy-absorption (Evans 1957).

A trajectorial picture is also available for the sagittal section. The load was applied to the highest point of the dome. As there are no satisfactory sagittal sections of frontoparietals of *Stegoceras* available for histological study it should only be mentioned that the force is transmitted towards the occipital condyle.

(3.) *Position of the occipital condyle and foramen magnum* - Schaffer and Reed (1972) and Stanley (1974) have elaborated on the functional significance of the reduction but not complete elimination of the moment arm about the occipital condyle in sheep and goats. A mechanical compromise has to be reached as reduction of the moment arm prevents severe flexion of the head during ramming and complete elimination would increase the tendency of sudden jolting movements with traumatic consequences. As examination of a sagittal section of a cast revealed, the line of action for a hypothetical impact force passes slightly beneath the occipital condyle and therefore the moment arm for the force producing flexion of the atlanto-occipital junction is short. Furthermore, if the position of the cervical column was horizontal, the moment arm of the force producing flexion at the intervertebral joints would have been short because the line of action would have extended close to the vertebrae. The impact vector is not precisely in line with the support vector of the cervical column (the ideal condition from a mechanical point of view and as indicated in

Galton's (1971: fig. 5) illustration).

The relative posteroventral displacement of the occipital condyle and foramen magnum is advantageous as the amount of deformation of the spinal medulla per degree of flexion or extension is minimized. Furthermore, there is an increase in the range of extension or flexion (Jenkins 1971).

Judging from the area of insertion, the *ligamentum nuchae* was well developed in the Pachycephalosauridae. Stanley (1974: 454) observed that in butting sheep slight flexion of the head would stretch the nuchal ligament and prolong the duration of the impact, thus acting (along with the powerful nuchal musculature) as an important shock absorber. This was probably also the case in the Pachycephalosauridae.

(4.) *Formation of an area suitable for frontal contact* - In the earliest known pachycephalosaurid, the lower Cretaceous species *Yaverlandia bitholus* Galton, 1971, there is a small dome-like thickening present on each frontal. In *Stegoceras* the thickening also affects the parietal and the sutures between the frontals and parietals become obliterated. The supratemporal fenestrae are reduced owing to invasion of the parietal. The thickening of the frontoparietal is most prominent in *Pachycephalosaurus*. The posterior extension of the possible area for contact presumably increased the possibility of variation in the angle between skull and cervical column as blows were delivered. Therefore, heads did not have to be precisely aligned prior to frontal contact.

The potential area for frontal contact is slightly convex transversely in most frontoparietals of pachycephalosaurids, indicating that self-correction for mis-aligned heads was not possible. This might suggest that frontal contact was not made by the ramming animals during high velocities (in contrast to "true rammers" like sheep and goats (Schaffer and Reed 1972)) but this is not necessarily the case as even in mountain sheep blows glance off quite frequently (Geist 1971). Another possibility of intraspecific combat would have been flank butting, which was probably also employed by pachycephalosaurids as the nasals are also somewhat thickened; the above mechanical considerations are also applicable for flank butting (Stanley 1974).

Conclusions of the functional analysis - It seems reasonable from the functional analysis to suggest that the thickened skull roof of *Stegoceras* and other pachycephalosaurids was employed in intraspecific combat (wrestling, pushing and/or ramming), probably between males. As the Recent marine iguana, *Amblyrhynchus* (Eibl-Eibesfeldt 1955) shows, reptiles are capable of such social interactions. In the mammalian "rammers", the structural modifications of the frontal region are very different. Each frontal is subdivided into dorsal and ventral tables, separated by the interpolation of a complex system of sinuses, which are separated by bony septa (Schaffer and Reed 1972). This adaptation is essential for the protection of the brain in these mammals. Owing to its much smaller dimensions, the pachycephalosaurid brain did not require such extensive protection and consequently structural modifications of the pachycephalosaurid skull are different from those seen in the Bovini.

PART TWO. APPENDICULAR SKELETON

1. Forelimb and pectoral girdle

Pectoral girdle and forelimb are well documented by the elements from the right side; only carpus and manus are entirely unknown.

Scapula (figs. 17 - 18) - The scapula is slightly damaged at its proximal and distal extremities. It is longer than the humerus. The blade of the scapula is slender and very narrow; it is slightly twisted along its length and bowed (following the outer contour of the thoracic ribs). The anterior margin of the blade is concave in lateral view while the posterior edge is almost straight. The anterior edge is rounded; the posterior edge is sharp, especially towards the proximal end. A small piece of the thin dorsal edge of the scapula shows a slightly irregular surface, possibly indicating the former presence of a cartilaginous susprascapula. The scapular blade has its maximum thickness immediately above the transition from the expanded base of the scapula. The lateral surface of the scapula shows a well-developed depression behind the anterior end of the base of the scapula. This concave surface extends diagonally upwards along the convex curve of the scapula and meets another depression continuing diagonally upwards from the glenoid region. The base of the scapula is strongly expanded relative to the narrow blade. The presence of an articular surface for a clavicle at the anterior end of the scapular base (as in *Hypsilophodon* (Galton 1974a: fig. 34)) cannot be determined as the corresponding region in the specimen under study is restored.

The scapula of *Stegoceras* is uniquely different from that of other ornithopods in its possession of an extremely narrow blade without any proximal expansion, resembling the condition in many theropod dinosaurs (*e.g. Allosaurus* (Gilmore 1920: fig. 40) and *Deinonychus* (Ostrom 1969: fig. 54 and Ostrom 1974: fig. 1)). The expanded base of the scapula closely resembles that of *Hypsilophodon* (Galton 1974a: figs. 34A, 35, 36A), *Dysalotosaurus* (Janensch 1955: fig. 31a) and *Thescelosaurus* (Galton 1974b: figs. 2G-H). A difference between *Stegoceras* on one hand and *Hypsilophodon* (Galton 1974a) and *Dysalotosaurus* (Janensch 1955) on the other is the fact that in the latter genera the scapula and the humerus are of equal length. However, in *Parksosaurus* (Parks 1926: fig. 7), *Iguanodon* (Casier 1960: fig. 18) and *Camptosaurus* (Gilmore 1909: 248, 250) the scapula is also longer than the humerus.

Coracoid (figs. 17 - 18, 20, A) - Except for its dorsal margin, the coracoid is a thin, plate-like bone. The inner surface is concave. Dorsally, it has a raised area penetrated by the coracoid foramen in the posterior half. The coracoid foramen (CO.F.) extends diagonally downwards and forwards (as in *Hypsilophodon* (Galton 1974a: 74) and *Dysalotosaurus* (Janensch 1955: fig. 32)); it is dorsally enclosed by the coracoid (not open as in *Camptosaurus* (Gilmore 1909: fig. 24)). A small but well-defined groove extends on the inner surface to the dorsal margin of the coracoid (fig. 20, A). The articular surface of the glenoid cavity (GL) is strongly expanded transversely.

Figure 17. *Stegoceras validus*, UA 2. Right scapula (SC) and coracoid (CO). Lateral view (partly restored). X 1.

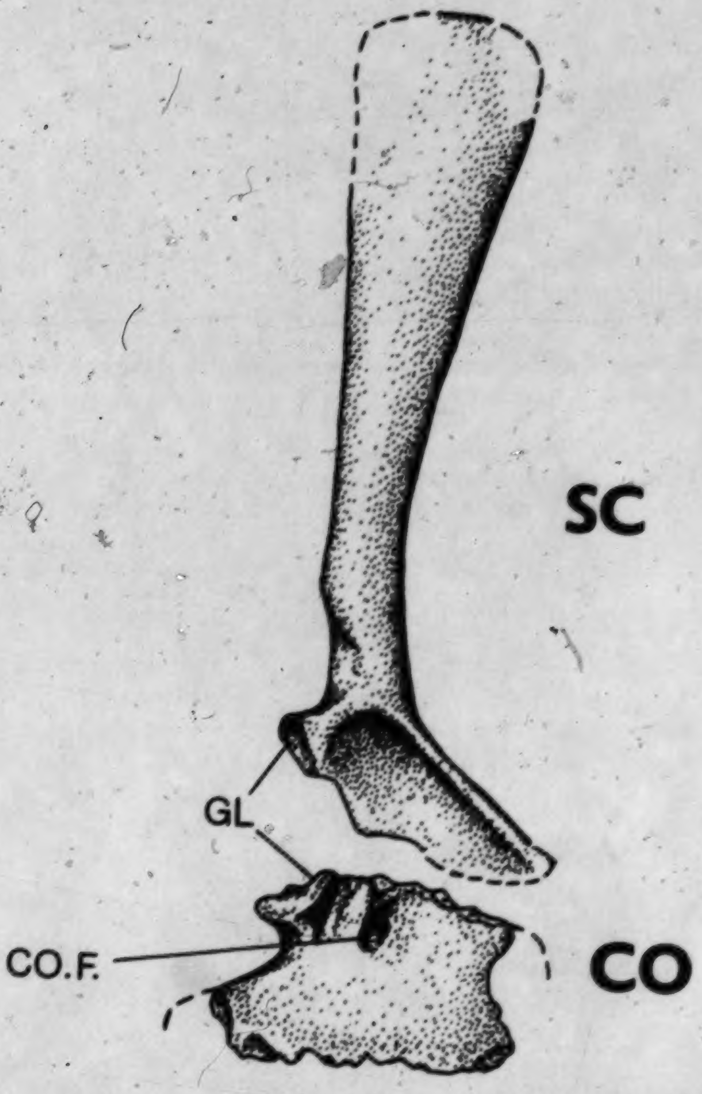
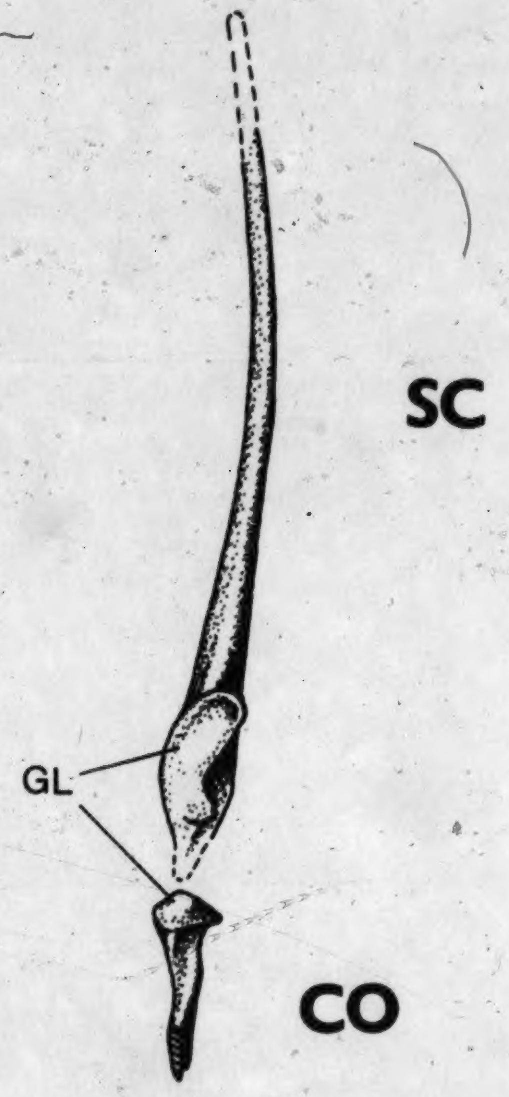

SC
GL
CO.F.
CO

Figure 18. *Stegoceras validus*, UA 2. Right scapula (SC) and coracoid (CO). Posterior view (partly restored). X 1.


SC
GL
CO

Much of the thin anterior and ventral edges of the coracoid is not preserved.

Humerus (fig. 19) - The humerus is slender and has a slightly twisted shaft; as a result of this, the long axis of the moderately expanded distal end is set at an angle to that of the broader proximal end. The distal end projects posteriorly beyond the posterior margin of the shaft. The deltopectoral crest (DP; fig. 19, B) is directed anteriorly and is situated on the proximal half of the humerus. Its development is responsible for the concave appearance of the proximal end in anterior view. The crest initially shows a relatively flat surface, which faces anterolaterally, then becomes more rounded distally and finally merges with the shaft of the humerus. The head of the humerus is situated in about the center of the proximal end of the humerus and is quite small. Radial and ulnar condyles seem to be separated by a shallow depression. In posterior view the inner margin of the humerus is gently concave, while the outer margin is gently convex.

The humerus of *Stegoceras* closely resembles that of other ornithopods and differs mainly in the weaker development of the deltopectoral crest (compared with *Hypsilophodon* (Galton 1974a: figs. 38 - 39)).

Ulna (fig. 20, C) - The proximal articular surface is triangular and expanded. It bears a moderately well developed olecranon process. Ridges extend from the proximal surface along the shaft of the ulna for some distance. The dorsal ridge continues to the rounded anterolateral edge of the distal end, the medial ridge to the sharp

Figure 19. *Stegoceras validus*, UA 2. Right humerus. (A) lateral view; (B) medial view. X 1.2.

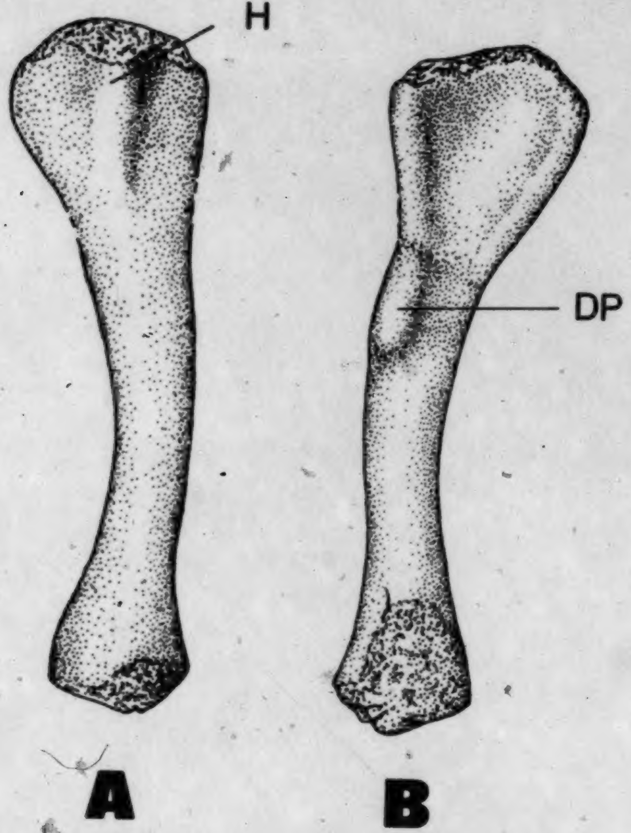
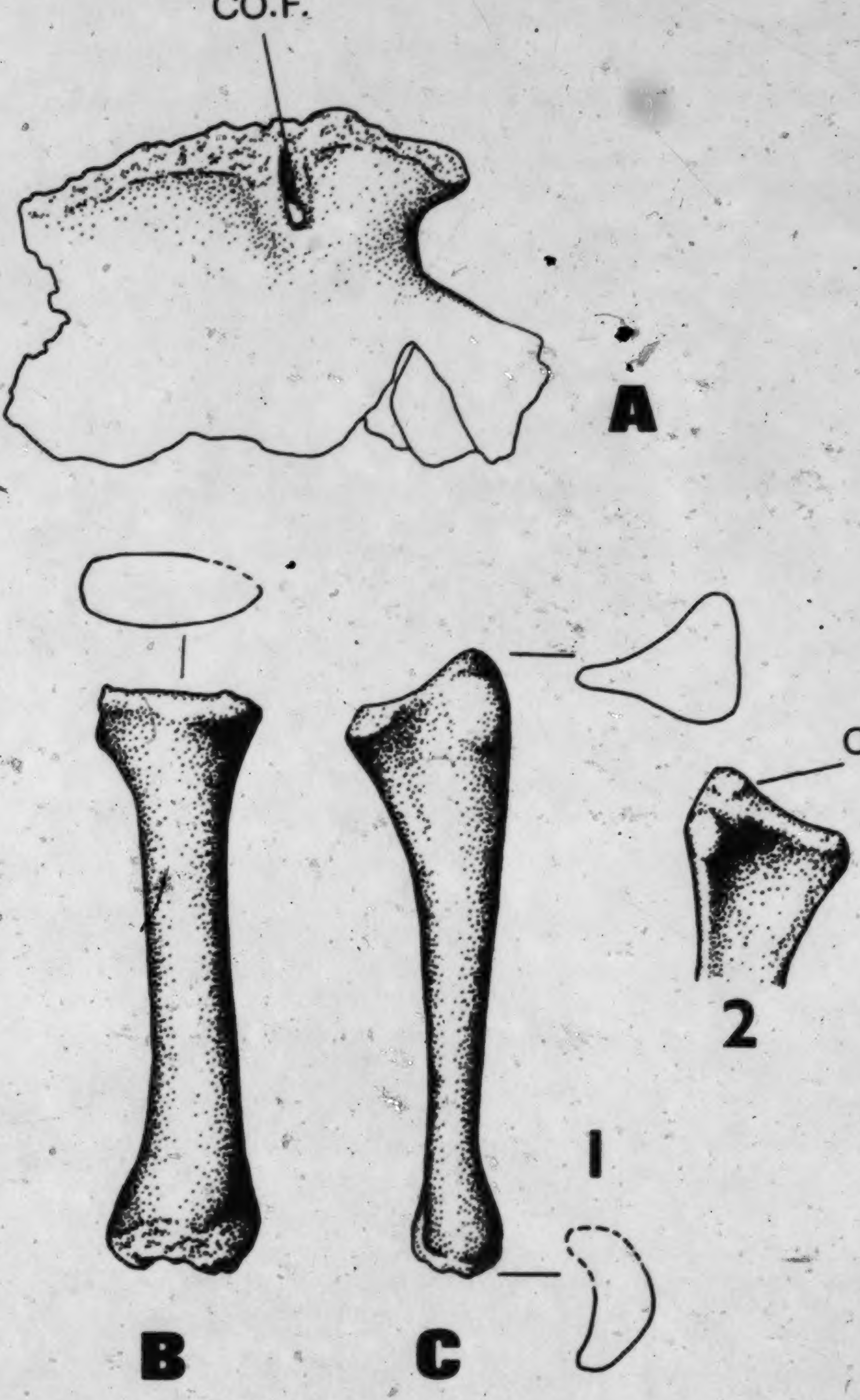

H
DP
A
B

Figure 20. *Stegoceras validus*, UA 2.

(A) right coracoid in medial view. X 1.8.

(B) right radius in lateral view, with outline of proximal articular surface. X 1.7.

(C) right ulna. (1) lateral view and (2) medial view, with outlines of articular surfaces. X 1.7.


CO.F.
A
OL
2
I
B
C

posteromedial edge and the lateral ridge continues along the shaft to merge with the convex lateral surface of the distal extremity. The shaft of the ulna is triangular in transverse section near the proximal end but becomes suboval at mid-length. The surface of the shaft is concave in medial view, with increasing concavity towards the distal end. The expanded distal end is laterally convex and medially concave; its long axis is almost perpendicular to that of the proximal end.

The ulna is very similar to that of other ornithopods such as *Hypsilophodon* (Galton 1974a: fig. 40), *Dysalotosaurus* (Janensch 1955: fig. 35) and *Nanosaurus* (?) (Galton and Jensen 1973: fig. 3D). It differs in the relationship of the proximal and distal ends (which are set at a smaller angle to each other in *Dysalotosaurus* and *Hypsilophodon*) and in being shorter relative to the humerus.

Radius (fig. 20, B) - The radius is unusual in being more heavily constructed than the ulna; only its proximal end is smaller than that of the ulna. The shaft is oval in transverse section. The proximal end of the radius is concave. The distal end is poorly preserved and its shape cannot be determined with certainty.

2. Hind-limb and pelvic girdle

The pelvic girdle is very broad (for a bipedal reptile) and widens posteriorly. Its only firm connection with the sacrum is above the acetabulum and is formed by the fourth and fifth sacral rib. The pelvic girdle of *Stegoceras* is documented by the right ilium and left ischium; the sacral rib mentioned by Gilmore (1924) could not be relocated.

Ilium (figs. 21 - 22) - The ilium is an elongate bone with equally long preacetabular and postacetabular processes. The anterior process is wide (in dorsal view) (fig. 22, C) and vertically thickened. Its lateral surface shows an anteroposteriorly extending depression, which is concave dorsoventrally. A prominent ridge is visible on the medial surface (fig. 22, A). Anteriorly the process becomes thinner but wider and slightly deflected ventrally. The posterior process is relatively straight. The pubic peduncle (PP; fig. 22) is extremely wide anteroposteriorly and (probably) transversely and is directed anteroventrally. The ischial head (ISH; fig. 22) is thick and rounded. Immediately behind the acetabulum, on the dorsal margin of the postacetabular process, there is a thin but wide horizontal process (antitrochanter) (AT; fig. 22). The acetabulum is relatively narrow. On the medial side of the ilium, about 15 mm above the highest point of the dorsal margin of the acetabulum, two well-defined depressions are visible (SR 4, SR 5; fig. 22, A). They probably represent the surfaces for the articulation of the fourth and fifth sacral ribs with the ilium (as in *Homalocephale* (Maryańska and Osmólska 1974: fig. $5A_4$)). Gilmore (1924: 35) claimed that three facets were present for the articulation of sacral ribs but I am not certain what Gilmore interpreted as the third facet. It is possible that the slightly crushed region immediately below the two other facets was interpreted by him as a third facet.

Figure 21. *Stegoceras validus,* UA 2. Right ilium (IL) and left ischium (IS) (reversed) in lateral view (restored), with transverse sections at various points. *Ca.* X 0.5.

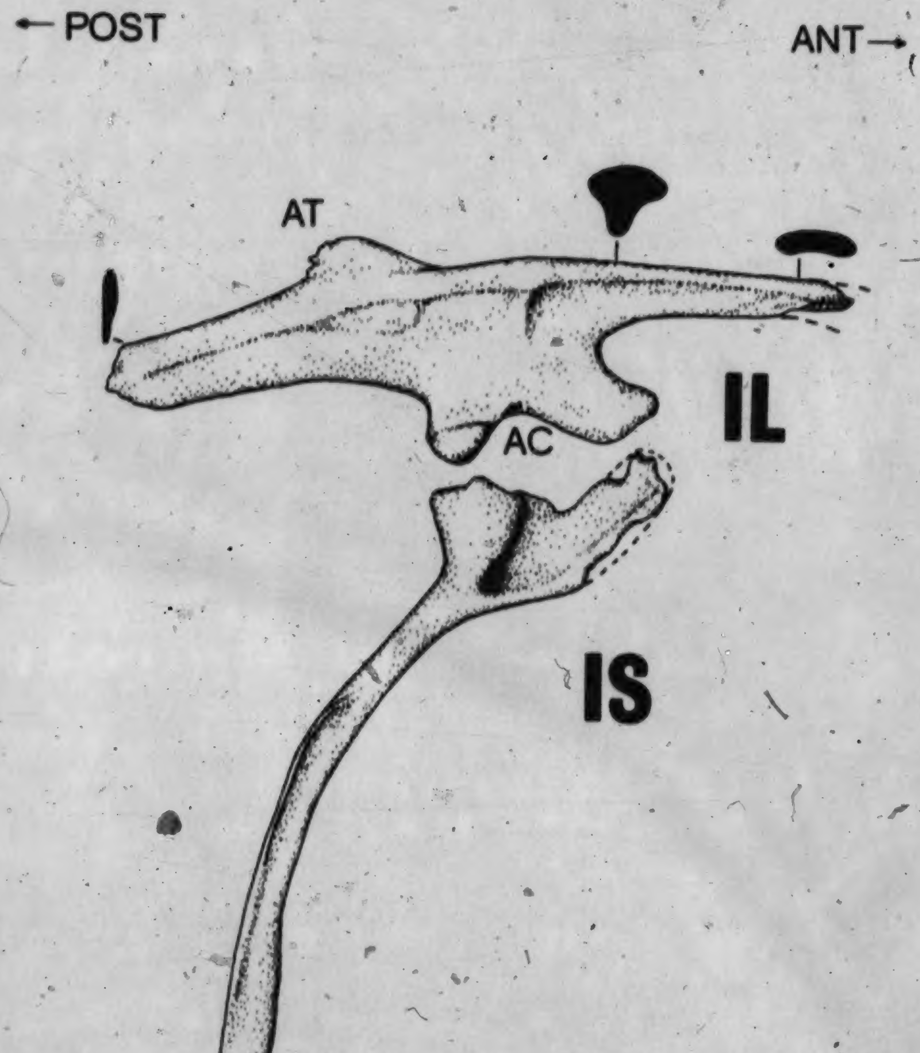
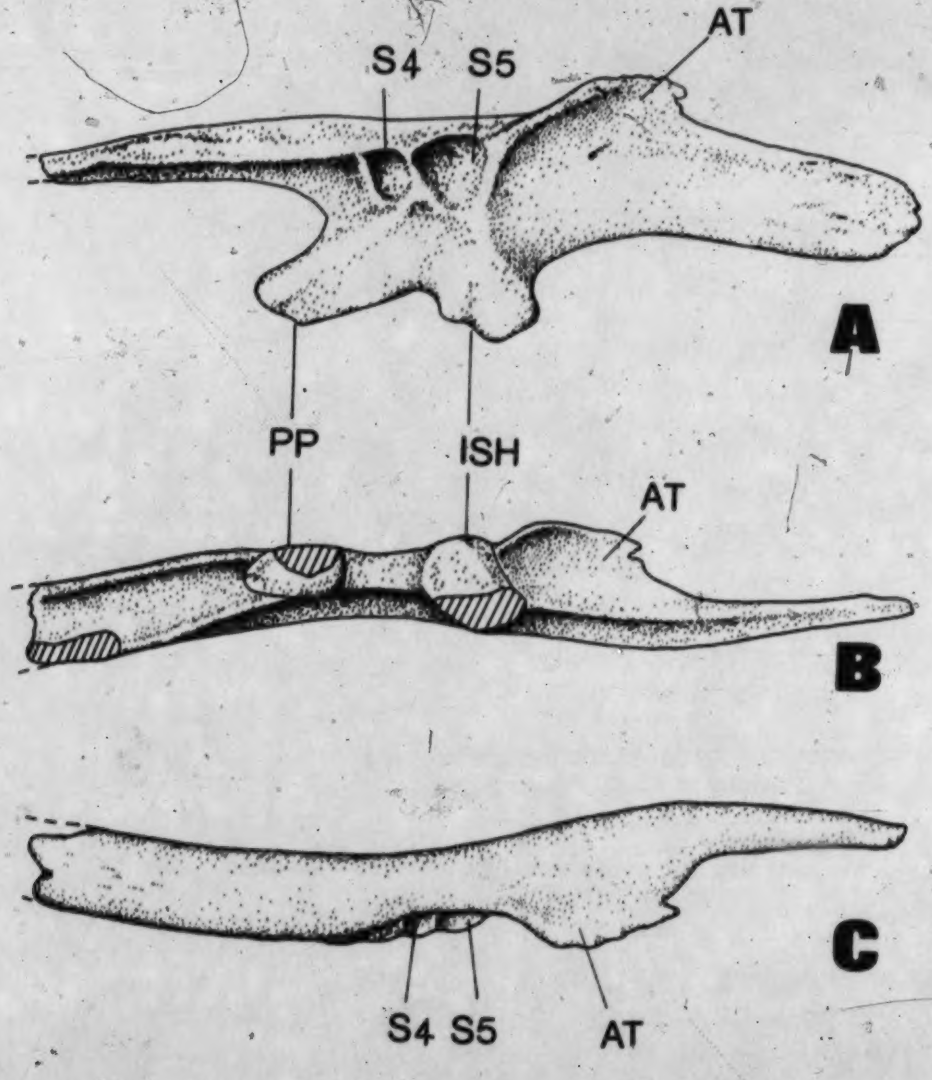

← POST
ANT →
AT
AC
IL
IS

Figure 22. *Stegoceras validus*, UA 2. Right ilium. (A) medial view; (B) ventral view; (c) dorsal view. *Ca.* X 0.6.


S4
S5
AT
A
PP
ISH
AT
B
C
S4
S5
AT

Ischium (fig. 21) - The ischium is a long and slender bone, with an expanded proximal portion with two peduncles and a curved shaft. The shaft is slightly turned inwards. An acute ridge extends along the median surface of the shaft. An obturator process is lacking. The posterior peduncle of the ischium is relatively short and stout and shows a broad articular surface. The incomplete anterior peduncle is unusually long and probably contacted the pubic peduncle of the ilium as in *Homalocephale* (Maryańska and Osmólska 1974: figs. 5A$_3$ and 5A$_4$; pl. 25, fig. 3b). The ventrolateral surface of the anterior peduncle is flat.

The pelvic girdle of *Stegoceras* closely resembles that of *Homalocephale* and is different from that of other ornithopods, especially in the apparent exclusion of the pubis from the acetabulum.

The hind-limb of *Stegoceras* is documented by both femora, an incomplete left tibia, the right fibula, four metatarsals of the right pes and four phalanges.

Femur - Both femora are badly crushed and incomplete. The description is based on both. The femur is slender and curved inwards. A moderately developed fourth trochanter is situated in the proximal half of the femur and is slightly pendant. The distal end shows two condyles, which are separated by an intercondylar groove (it appears to be deep owing to crushing in this region of the bones). The lateral condyle is more strongly developed than the medial condyle.

The femur is similar to those of *Homalocephale* and *Prenocephale* (Maryańska and Osmólska 1974). The position of the fourth trochanter on the proximal half of the femur is also seen in *Hypsilophodon* (Galton 1974a: fig. 54) and *Dryosaurus* (?) (Galton 1975: fig. 3A-D) but not in iguanodontids (*Iguanodon* (Casier 1960: fig. 20); *Tenontosaurus* (Ostrom 1970: pl. 20, figs. D - E)).

Tibia - The tibia is only represented by a very fragmentary left element. The shaft is slender and twisted, probably indicating that the articular surfaces were set at an angle to each other. Structural details of the proximal end of the tibia given by Gilmore (1924: 37) cannot be verified as this region is restored in colored plaster.

Fibula (fig. 23, A) - Only the right fibula is still available for study. It is a slender bone. The proximal end is relatively wide (as in *Dysalotosaurus* (Janensch 1955: fig. 40 and pl. 14, fig. 4)) and set at an angle to the thin distal extremity. The posterior surface of the distal region is flattened (for contact with the anterior surface of the tibia). The inner edge of this part of the fibula is sharp, whereas the outer edge is rounded.

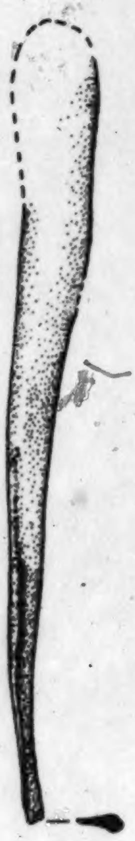
Metatarsals - Four metatarsals of the right pes are preserved; only metatarsal I (fig. 24, A) is well preserved and complete. The first metatarsal is reduced; it is curved and splint-like. Its proximal part is narrow and compressed, whereas the distal end is thickened and forms a subtriangular surface for the articulation with the

Figure 23. *Stegoceras validus*, UA 2.

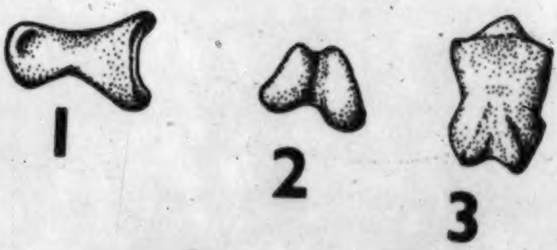
(A) right fibula, with transverse section near distal end. X 0.7 (section: X 1).

(B) phalanx 4 of digit IV (right pes). X 1.2.
(1) lateral view; (2) distal articular surface; (3) dorsal view.

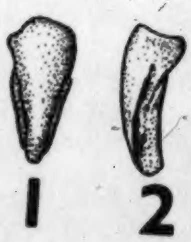
(C) ungual of digit IV (right pes). X 1.
(1) dorsal view; (2) lateral view.



A



B



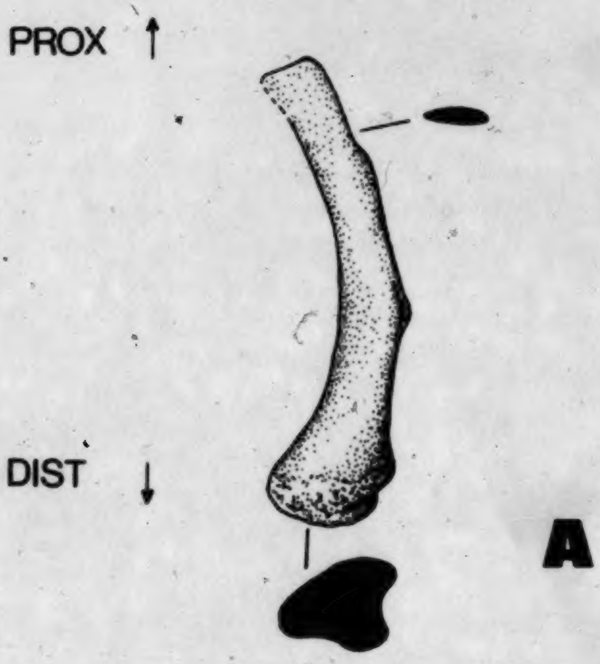
C

Figure 24. *Stegoceras validus*, UA 2.

(A) right metatarsal I in lateral view.

(B) phalanges 1 and 2 of digit IV (right pes) in lateral view and with distal and proximal articular surfaces, respectively.

All X 1.2.


PROX ↑
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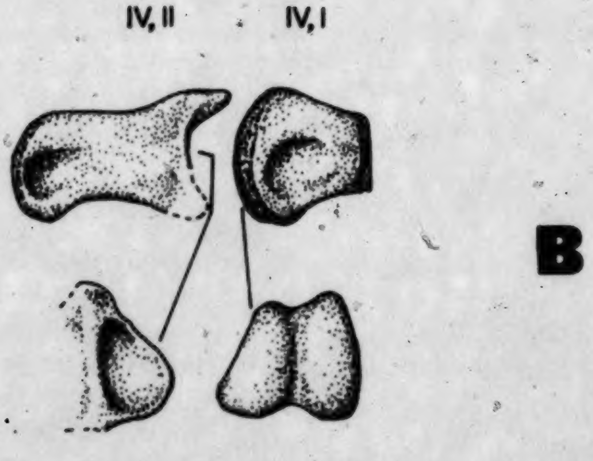
A

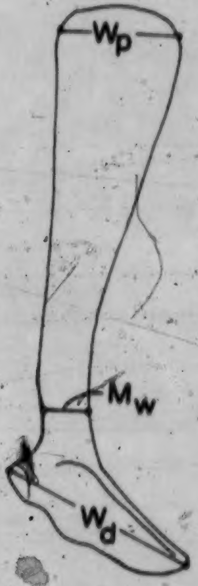

IV, II
IV, I
B

phalanges. The flattened proximal extremity probably contacted the dorsolateral surface of the metatarsal II. The distal surface of metatarsal II is roughened. The anterolateral side of metatarsal III is flat and extends obliquely dorsomedially; it probably formed the area for contact with the fourth metatarsal. The shaft of metatarsal IV is subtriangular in transverse section. Its distal articular end was apparently obliquely inclined.

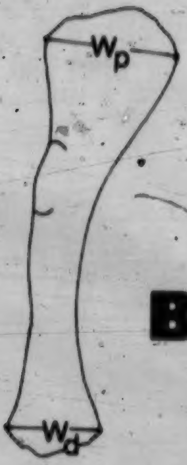
Although metatarsals II to IV are incompletely preserved it appears that they closely fitted together, resulting in a relatively narrow metatarsus. Metatarsal III was the largest metatarsal (as in other ornithopods).

Phalanges - The distal end of a phalanx, two phalanges and one ungual are available for study. Gilmore's tentative identification of these bones as elements of digit IV of the right pes is accepted in this paper. The distal end belongs to the proximal phalanx (1) of the digit (fig. 24, B). It does not differ from phalanx 1 of digit IV in *Homalocephale* (Maryańska and Osmólska 1974: pl. 30, fig. 6) in structural details. The fragment indicates a short and stout phalanx. The *fovaeae ligamentosae* are well developed. The distal region of the phalanx is dorsoventrally flattened. The distal articular surface shows two distinct condyles, separated by a median vertical depression. The proximal end of the almost complete phalanx 2 (fig. 24, B) shows a corresponding ridge on its articular surface. The latter is subdivided by the ridge into two surfaces. Furthermore, a dorsal process of the proximal end of phalanx 2 fits into the dorsal continuation of the depression on the distal articular end of the preceding phalanx. The third phalanx (fig. 23, B) is determined as the penultimate phalanx (4) of the digit because its distal articular surface articulates exactly with the proximal surface for interphalangeal articulation of the ungual (phalanx 5). The ungual (fig. 23, C) is quite slender and slightly curved. A groove extends longitudinally on each side of the claw to the pointed tip.

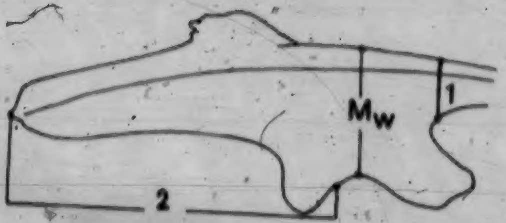
Figure 25. Diagram illustrating some of the distances used in Table 2. (A) scapula; (B) humerus; (C) ilium; (D) ischium.



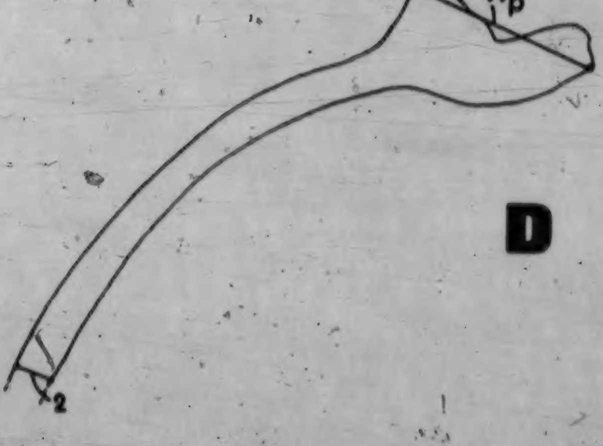
A



B



C



D

Table 2

Measurements of the appendicular skeleton

(in mm; see diagram for distances)

Element	L	W_p	W_d	M_w	1	2
Scapula	130*	25*	45*	11	-	-
Humerus	86	24	17	0	-	-
Radius	50	13	12	6	-	-
Ulna	54	14	11	5	-	-
Ilium	210*	-	-	40	23	112
Ischium	195*	60*	-	-	-	11
Femur	225*	40*	-	-	-	-
Tibia	220*	50*	60*	-	-	-
Metatarsal I	57	7	14	6	-	-
Digit IV, phalanx 1	-	-	15	-	-	-
Digit IV, phalanx 4	18	12	12	-	-	-
Digit IV, ungual	21	10	-	-	-	-

*estimated

3. Myology of the pelvic region and hind-limb

The pelvic musculature of ornithopod dinosaurs has been extensively discussed by Romer (1927), Janensch (1955) and, most recently, by Galton (1969). Their detailed accounts have been used in reconstructing the pelvic musculature of *Stegoceras*. It is difficult to make such a restoration as the structure of the pachycephalosaurid pelvic girdle differs significantly from that of typical ornithopods. The discussion is subdivided according to functional units, with nomenclature mainly after Romer (1927).

Extensors of the tibia

The *M. ilio-tibialis* probably originated on the narrow dorsolateral surface of the ilium. It cannot be determined whether the muscle was divided into two (as in lizards) or three parts. The muscle is responsible for a small amount of adduction and abduction of the leg (Galton 1969). The outward curvature of the preacetabular part of the ilium provided a mechanically advantageous more anteroposterior line of action.

The origin of the *M. ambiens* cannot be determined as the pubis is unknown in *Stegoceras*.

The *M. femoro-tibialis* originated in the distal half of the femur as in *Hypsilophodon* (Galton 1969: 13 - 14) and a tripartite subdivision is indicated by the surface markings.

All three muscles presumably inserted on the cnemial crest of the tibia, perhaps in a common aponeurosis.

Protractors of the femur

The *M. ilio-femoralis externus* probably originated from a roughened area on the lateral side of the ilium in a position comparable to that of the antitrochanter in hadrosaurs (considered to be the area of origin for this muscle in that group by Romer (1927, fig. 20)). The muscle presumably inserted on the (not preserved) lesser trochanter of the femur. It helped to prevent disarticulation of the femur.

Owing to the absence of a pubis the orientation of the *M. ilio-femoralis internus* cannot be discussed.

Flexors of the tibia

The origins and insertions of the *M. ilio-fibularis* and *M. ischio-flexorius* are not preserved.

Retractors of the femur

The *M. ilio-trochantericus* probably originated from a depression on the lateral surface of the preacetabular process of the ilium and presumably inserted onto the greater trochanter.

The *M. caudi-femoralis longus* and *brevis* (*sensu* Galton 1969) inserted on the fourth trochanter (as in *Hypsilophodon* (Galton 1969: figs. 8 - 10)). On the inner side of that trochanter there is a well-developed concave area for insertion of the *M. caudi-femoralis longus*. The *M. caudi-femoralis brevis* probably inserted on the lateral surface of the fourth trochanter. As a brevis shelf (*sensu* Romer) is not developed on the postacetabular portion of the ilium in *Stegoceras*, the *M. caudi-femoralis brevis* presumably originated along the posterolateral margin of the ilium and, in addition, on the centra of the last sacral and the first caudal vertebra (as in *Alligator* (Galton 1969: 18)). The *M. caudi-femoralis longus* probably originated on the lateral surface of the centra and the ventral surface of the transverse processes of the anterior caudal vertebrae (as in other ornithopods (see Romer 1927)).

The *M. obturator internus (= M. pubo-ischio-femoralis externus, pars anterior)* probably had its origin on the lateral surface of the ischium. This surface shows a groove, which is posterodorsally limited by a well-developed ridge and becomes shallower distally. An obturator process is absent. The area of insertion cannot be determined owing to the poor preservation of the femora.

The *M. adductor femoralis* probably originated from the dorsal part of the ischium and apparently inserted close to a faint rugose line between the fourth trochanter and the outer condyle (similar to the area of insertion in *Hypsilophodon* (Galton 1969: figs. 8A, 9B)).

The *M. ischio-trochantericus* presumably had its origin on a well-defined flattened surface internal to the dorsal margin of the ischium and a more distally situated shelf-like expansion of the ischial shaft. It probably inserted close to the head of the femur (as in *Thescelosaurus* (see Romer 1927: figs. 14 - 18)).

Axial musculature

As the pubis is unknown in *Stegoceras* a restoration of the axial musculature has not been attempted. Only a few comments based on the study of the remainder of the pelvic girdle are included.

The more superficial part of the dorsal axial musculature probably attached to the preacetabular process of the ilium. The *M. dorsalis trunci* presumably inserted onto the wide dorsomedial surface of this process. This surface is marked by numerous faint, longitudinal striations.

The abdominal cavity was probably very large as indicated by the considerable transverse dimensions of the rib cage and the broad pelvic girdle (as in *Homalocephale* (Maryańska and Osmólska 1974: fig. 5A)). It certainly needed strong support and Maryańska and Osmólska (1974: 96) suggested that a well-developed *M. obliquus abdominis* inserted on the anterior margin of the ischium.

4. Locomotion

Although the ratios given by Galton (1974b: table 2) are not precisely accurate (being based on Gilmore's paper, which does not indicate the fact that the measurements are in part merely estimations), they clearly show that *Stegoceras* is non-cursorial, most closely comparing with the iguanodontids (*s. l.*) *Camptosaurus* and *Tenontosaurus*.

The distal segments of the hind-limb are not elongated as in hypsilophodontids but rather the tibia is slightly shorter than the femur in *Stegoceras*. Unfortunately, the manus is unknown in the Pachycephalosauridae; therefore, it cannot be decided whether *Stegoceras* resembled *Thescelosaurus* in being more habitually quadrupedal than other small to medium-sized ornithopods. However, the forelimb and pectoral girdle are relatively weakly constructed and the size disparity between forelimb and hind limb indicates that *Stegoceras* was mainly bipedal.

PART THREE. POSTCRANIAL AXIAL SKELETON

1. Osteology

The vertebral column of *Stegoceras* is only documented by two dorsal and eight caudal vertebrae (from different regions of the tail).

Dorsal vertebrae (figs. 26, 27, A) - There are two well-preserved dorsal vertebrae. In discussing the position of these vertebrae in the dorsal column, Gilmore (1924: 28) pointed out that the horizontal orientation of the zygapophyses appears to indicate that the vertebrae represented posterior dorsals but he considered them as mid-dorsal vertebrae based on the marked upward curvature of their diapophyses. Maryańska and Osmólska (1974: 86) pointed out that this argument is not valid. Comparison of the dorsal vertebrae of *Stegoceras* with illustrations of those in *Homalocephale* (Maryańska and Osmólska 1974: fig. 4) reveals that they most closely resemble "dorsal n + 8" and "dorsal n + 9" (third and second dorsal vertebra, respectively, counted from the sacrum; see Maryańska and Osmólska (1974: fig. 4B-C)) of *Homalocephale*. In the specimen NMC 8537 of *Thescelosaurus neglectus* (Sternberg 1940: 485 (*"T. edmontonensis"*)) the angle between the diapophysis and the horizontal plane also increases posteriorly (however, this is not the case in other specimens of *Thescelosaurus* (Galton 1974b: 1058)). The two vertebrae of *Stegoceras* probably represent posterior dorsals, that with the narrower neural spine being from a more anterior position. The centra are amphiplatyan. The ventral margin is moderately concave (in lateral view) and is sharply rounded, lacking a keel. The lateral surfaces of the centrum are concave anteroposteriorly. The suture between the neural arch and the centrum is on the level of the floor of the large neural canal. The neural spine is tall and subrectangular, slightly increasing in thickness (in transverse direction) towards the dorsal extremity. The diapophyses are strongly curving dorsally and slightly posteriorly. The zygapophyses are broad and relatively short. Their articular surfaces are almost horizontal, those of the postzygapophyses slightly facing outwards and those of the prezygapophyses slightly facing inwards. Anteroventral to each postzygapophysis, the posterior surface of the pedicle of the neural arch is deeply excavated. Most notable is the tongue-and-groove-like pattern of interzygapophyseal articulation (fig. 26). The prezygapophysis shows two corresponding ridges. This remarkable arrangement is elsewhere only known in *Homalocephale* (Maryańska and Osmólska 1974: 85). [Brown and Schlaikjer (1943: 145) claim that "there is also an indication of this in some of the *Protoceratops* dorsals"; in their description of the dorsal vertebrae of *Protoceratops*, however, Brown and Schlaikjer (1940: 217 - 218) did not mention this feature.]

Caudal vertebrae - anterior vertebrae - The most anterior caudal vertebra (fig. 27, B) is almost complete, only lacking the posterior part of the neural arch. Its anterior articular surface slightly protrudes anterodorsally and is markedly concave. In *Homalocephale* (Maryańska and Osmólska 1974: 87) this feature is restricted to the first caudal vertebra, supporting Gilmore's

Figure 26. *Stegoceras validus*, UA 2. Posterior dorsal vertebra (slightly restored). X 1.9. (A) ventral view; (B) dorsal view.

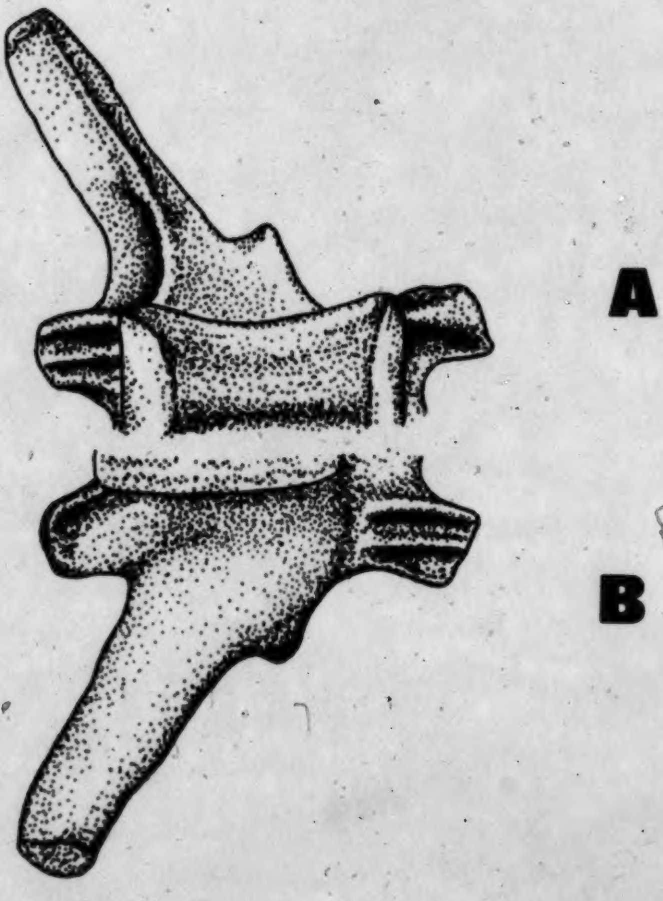

A
B

Figure 27. *Stegoceras validus*, UA 2. X 1.3.

(A) posterior dorsal vertebra in lateral view.

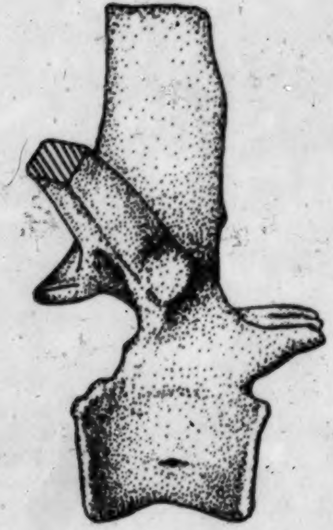
(B) first caudal vertebra with left caudal rib.

(1) lateral view; (2) anterior view;

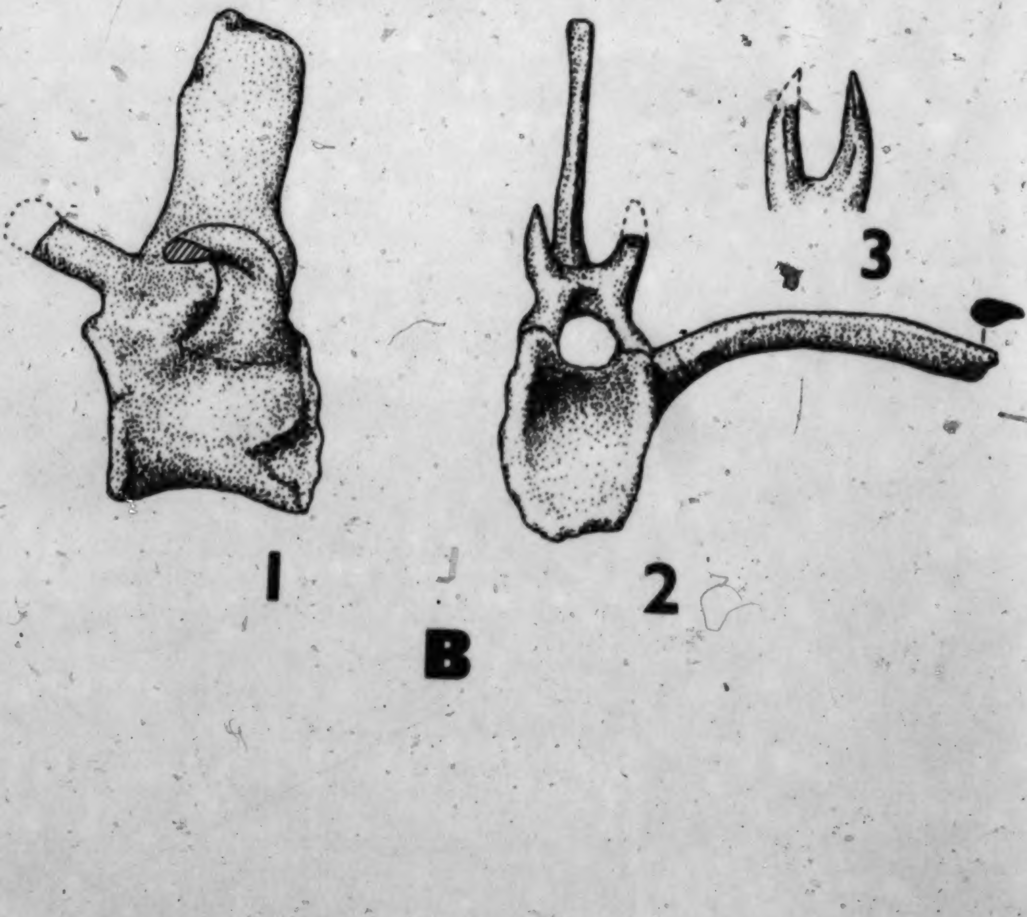
(3) prezygapophyses in dorsal view.

(C) mid-caudal vertebra in lateral view, with transverse section near the anterior surface of the centrum.

(D) posterior caudal vertebra in lateral view.



A



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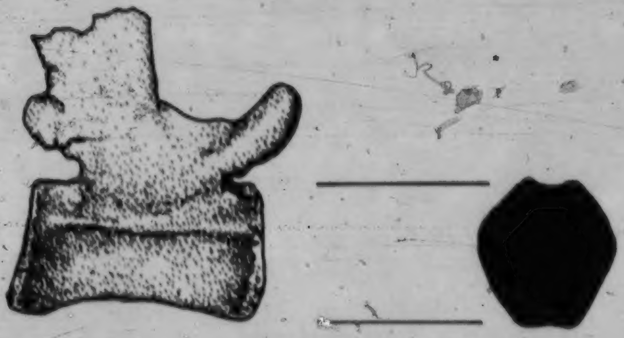

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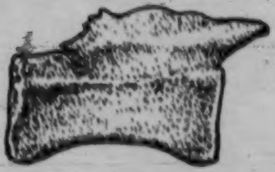


D

determination of the vertebra under discussion as the first caudal. Facets for the chevron are lacking on the posteroventral margin of the centrum. The lateral and ventral surfaces of the centrum are concave anteroposteriorly. The neural arch is compressed laterally and positioned well forward relative to the centrum. The quadrangular neural spine is high, compressed and has sharp anterior and posterior edges; it becomes slightly thickened dorsally. The prezygapophyses project anterodorsally, well beyond the anterior articular surface of the centrum. They are positioned close to each other and show strongly inclined, almost vertical surfaces for articulation. The left caudal rib is partly preserved, lacking the distal extremity. It is narrow, flattened and rises upwards proximally. The rib extends relatively straight out from the centrum.

The other anterior caudal vertebra has been interpreted as a third (Gilmore 1924: 29) or fifth (Maryańska and Osmólska 1974: 87) caudal. As it shows well-defined facets for chevrons and such facets first occur on the fifth caudal in *Homalocephale*, I follow Maryańska and Osmólska's determination. The centrum is oblique in lateral view, the anterior surface for intercentral articulation being situated higher than the posterior one. The centrum is much shorter than in the first caudal vertebra. Its lateral and ventral surfaces are concave anteroposteriorly. The lateral surfaces are marked by a small pit-like depression at about mid-length. In comparison with the corresponding structures of the first caudal, the fifth caudal vertebra differs in the following features:

a) neural spine narrower (anteroposteriorly);

b) prezygapophyses further apart from each other;

c) caudal rib less arched, becoming almost straight (as in *Homalocephale* (Maryańska and Osmólska 1974: 86));

d) presence of well-defined facets for chevron.

Mid-caudal vertebrae (fig. 27, C) - Three vertebrae seem to be referable to this group. They differ from the anterior caudal vertebrae described above in having more elongated centra and smaller, more posteriorly situated neural spines, lacking caudal ribs and showing a hexagonal outline of the articular surfaces of the centra. The latter is produced by longitudinal ridges on the ventral and lateral surfaces of the centra. The neural spine is very thin and strongly compressed laterally. The length of the centra slightly decreases from the first to the third of the preserved vertebrae.

Posterior caudal vertebrae (fig. 27, D) - Three vertebrae of subequal size probably represent posterior caudals. The neural spines are very reduced. The lateral and ventral surfaces of the centra show longitudinal ridges. The prezygapophyses are closer together than on the mid-caudal vertebrae. The postzygapophyses are very small. The neural spines are more posteriorly situated than on the preceding caudals and are connected to the junction of the prezygapophyses by a sharp and thin median ridge.

Table 3

Measurements of the vertebrae

(in mm)

Vertebra	Ghc	Glc	Gwc
DV A**	16	20	15
DV B**	16	21	16
CV 1	17	22	17
CV 5	18	19	19
MCV A**	16*	27	19
MCV B**	16*	26	17
MGV C**	15	25	15*

[*] estimated

[**] letter indicating relative position of vertebra (A more anterior than B, etc.)

Chevrons - Several fragments and one almost complete element (fig. 29, B) are available for study. The latter is probably from an anterior caudal vertebra and only lacks the distal extremity. The articular ends are slightly expanded and not connected with each other as in the anterior chevrons of *Camptosaurus* (Gilmore 1909: fig. 20), *Dysalotosaurus* (Janensch 1955: pl. 13, figs. 16 - 18) and *Hypsilophodon* (Galton 1974a: figs. 28B and 30B).

Ribs - Thirteen incomplete right and eight incomplete left thoracic ribs, two cervical ribs and one sacral rib have been reported by Gilmore (1924) in UA 2. It is not clear which specimen was determined as a sacral rib by Gilmore (1924: 31) as he does not figure it and none of the specimens studied even resembles a sacral rib.

Cervical ribs - The more complete specimen probably represents the posteriormost left cervical rib. The capitular process and the distal extremity are not preserved. It resembles the eighth cervical rib of *Camptosaurus* (Gilmore 1909: fig. 21) and *Hypsilophodon* (Galton 1974a: fig. 19).

Thoracic ribs - As far as preserved, all thoracic ribs appear to have been double-headed. Capitulum and tuberculum are distinct and articulate with the diapophysis. The tuberculum is always placed laterally and posteriorly relative to the capitulum.

A left rib, provisionally determined as the first thoracic rib by Gilmore (1924: 31), is relatively straight and wide. The following three ribs (from the right side) increase in length, reaching a

Figure 28. *Stegoceras validus*, UA 2. Caudal tendons. X 1.

(A, B) Gilmore's "type 4".

(C) Gilmore's "type 3".

(D) Gilmore's "type 2".

(E) Gilmore's "type 1".

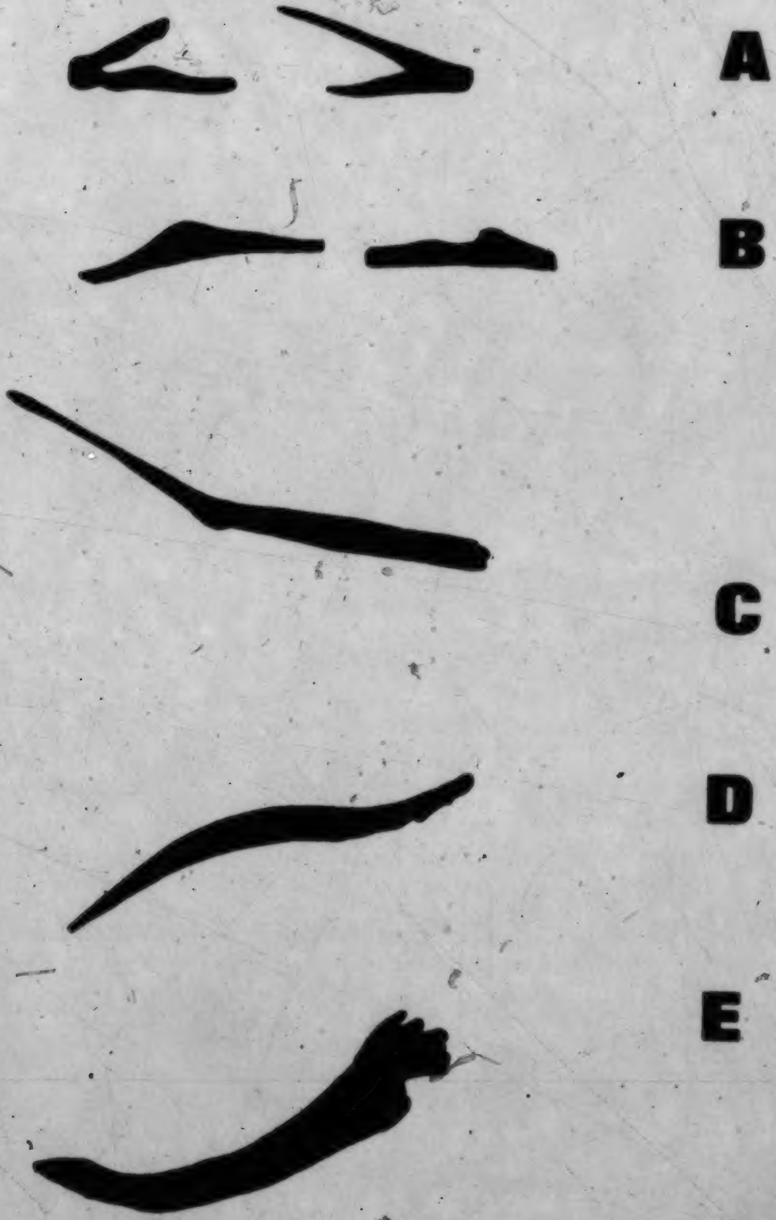
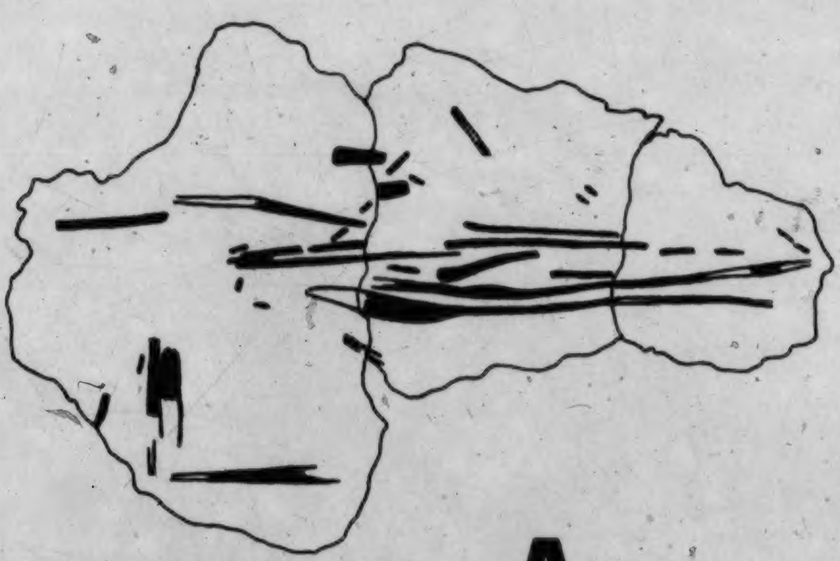

A
B
C
D
E

Figure 29. *Stegoceras validus*, UA 2.

(A) caudal tendons in the matrix. X 0.8.

(B) chevron in anterior view. X 2.



A

B

maximum at the fourth rib, and become more curved. Posterior to the fourth rib, they become increasingly more curved and slender. The capitular and tubercular facets become smaller; the capitular process increases slightly in length and (in transverse section) changes from a flattened to a subcircular process. The five posteriormost ribs are characterized by a longitudinal depression extending along the shaft on the anterior edge of the rib, disappearing at about mid-length.

Caudal tendons (figs. 28 - 29) - Gilmore (1924) described a large number of rib-like elements as "abdominal ribs" (p. 31) and others as "ossified tendons" (p. 32). Thus, the possession of "abdominal ribs" was thought to be a unique character in *Stegoceras* as no other ornithischian shows such elements. The discovery of a basket-like arrangement of ossified tendons around the posterior part of the tail in *Homalocephale* (Maryańska and Osmólska 1974: pl. 28, figs. 3 - 4) lead Maryańska and Osmólska (1974: 93) to challenge Gilmore's interpretation.

I have attempted to identify the six types of elements listed by Gilmore with homologous parts of the caudal tendons in *Homalocephale:*

Type 1 (fig. 28, E): "Large, heavy, sinuous segments with more or less flattened ends that are sometimes grooved with ray-like points" (Gilmore 1924: 31). These elements correspond to the thickened medial portions of the tendons from the fourth and fifth row of the caudal "basket" in *Homalocephale*.

Type 2 (fig. 28, D): "Smaller, subround, sinuous segments having both ends slightly flattened and slenderly pointed" (Gilmore 1924: 32). These elements appear to be similar to the medial portions of the tendons from the second and third row of the caudal "basket" in *Homalocephale*.

Type 3 (fig. 28, C): "Of about the same size as the second [type], subround, sinuous, with one flattened end, the other drawn out into a slender attenuated rod-like process" (Gilmore 1924: 32). This type clearly includes more posterior parts of the tendons represented by type 2.

Type 4 ((fig. 28, A - B): "Small, with long bifurcated divergent round processes at one end, the other end unknown, ..." (Gilmore 1924: 32)) and type 5 are not clearly matched by any tendon illustrated or described by Maryańska and Osmólska. Type 5 was characterized by its asymmetry and might include pathological specimens and/or larger elements of type 4. Perhaps the rod-like posterior parts of the caudal tendons fused to each other and type 4 could be explained as representing such connections.

Finally, Gilmore's "ossified tendons" represent the thin posterior extremities of the caudal tendons (fig. 29, A). A small block of sandstone (preserved in three pieces) containing parts of the tail basket is catalogued under UA 2 but has not been mentioned by Gilmore. Presumably parts from the inner rows are preserved, some of them still in their original arrangement. The specimen beautifully demonstrates the connection between the thickened medial and rod-like posterior portions of the caudal tendons. A second block, partially embedded in plaster, also contains parts of the caudal basket, including elements of Gilmore's types 1 and 2.

2. The functional significance of the interzygapophyseal articulations

Gilmore (1924: 28) was impressed by the elaborate tongue-and-groove articulations between the zygapophyses of succeeding dorsal vertebrae in *Stegoceras* but did not offer a functional explanation. This peculiar type of articulation has since only been documented in another pachycephalosaurid, *Homalocephale* (see Maryańska and Osmólska (1974: 85)). In both cases, only posterior dorsal vertebrae are known but presumably this condition occurred also in other regions of the presacral vertebral column.

This unique feature clearly prevents any significant lateral movement (at least of the posterior part) of the presacral column, thereby providing great rigidity. If the assumption of the head butting-model is correct, force transmission during the impact would take place through the dorsal and cervical vertebral column. Lack of rigidity would result in dislocation of vertebrae with traumatic consequences. The most parsimonious mechanical solution (paradigm *sensu* M. J. S. Rudwick) is a solid bar, which, of course, is not a desirable solution. The tongue-and-groove articulation approaches the paradigm in providing rigidity by preventing significant lateral flexion of the column during the conduction of forces resulting from impacts.

The rigid nature of the vertebral column (probably enhanced by ossified tendons as in other ornithopods) furthermore seems to indicate that it was held almost horizontally during locomotion (as postulated by Galton (1970b) for ornithopods in general).

3. The functional significance of the caudal tendons

It is evident that the tail in pachycephalosaurids was highly specialized for a particular function. The ensheathing tendons made much of the tail rigid, enhancing the effect of the almost vertical articular surfaces of the zygapophyses in the caudal vertebrae. The marked inclination of the articular surfaces restricted lateral flexion (as do the long caudal ribs in the anterior region of the tail). The basket-like arrangement of the ossified tendons probably inhibited significant vertical movements in the more posterior part of the tail to a certain degree but is still relatively elastic.

Superficially, it might appear that the pachycephalosaurid tail might have acted as a dynamic stabilizer as in *Deinonychus* (Ostrom 1969) but this seems improbable as *Stegoceras* does not show any cursorial adaptations and a dynamic stabilizer is only meaningful in cursorial forms. Frequently, lesions are visible on the thick medial portions of the tendons of *Stegoceras* (and *Homalocephale* (see Maryańska and Osmólska 1974: 99)), indicating that the tail served a different function. Maryańska and Osmólska envisage the tail acting as a prop during rest, when a more upwardly inclined posture of the vertebral column and pelvic girdle was achieved; this posture would

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result in placing the center of gravity behind the acetabulum. This interpretation appears reasonable and is accepted here *faute de mieux*.

PART FOUR

NOTES ON THE BIOLOGY OF *STEGOCERAS* AND OTHER PACHYCEPHALOSAURIDS

Stegoceras is relatively rare in the classical collection sites of the Judith River Formation and, with the exception of UA 2 and NMC 138; only isolated frontoparietals have been found. Many of them show signs of transport. Perhaps *Stegoceras*, like certain other dinosaurs, lived in upland regions (which have not been sampled). The Mongolian pachycephalosaurids have been found in sandstones, which apparently were formed in such a sedimentary regime.

The dentitions clearly show that pachycephalosaurids were herbivorous. The endocranial cast of *Pachycephalosaurus* (Brown and Schlaikjer 1943) and the data from *Homalocephale* and *Prenocephale* (Maryańska and Osmólska 1974) indicate that the *N. olfactorius* and *N. opticus* were well-developed, suggesting (together with the large external narial cavity and orbit) a good sense of olfaction and vision. These senses might have been important in the detection of predators as pachycephalosaurids lack any protective armor and presumably were not capable of fast escape. It is unlikely that the thickened frontoparietal was used as a defensive weapon (as has been suggested by Maryańska and Osmólska (1974: 99)).

The large abdominal cavity and the broad pelvis might indicate viviparity (Maryańska and Osmólska 1974) but in my opinion could also be related to the herbivorous habits of pachycephalosaurids (requiring a large intestinal tract (as in other herbivorous vertebrates)).

PART FIVE

1.. The status of the Pachycephalosauridae from North America and East Asia

A. East Asia

Maryańska and Osmólska (1974) described three new monotypic genera from the Upper Cretaceous of Mongolia: *Tylocephale* (type species: *T. gilmorei*) from the Barun Goyot Formation (Campanian) and *Homalocephale* (type species: *H. calathocercos*) and *Prenocephale* (type species: *P. prenes*) from the Nemegt Formation (Maastrichtian).

Tylocephale gilmorei is documented by an incomplete skull and a partial mandible. The species is characterized by the structure of the posterior region of the skull. The dome reaches its highest elevation far posteriorly and is even visible in occipital view. The posterior cheek region shows extreme lateral expansion. The orientation of the quadrate and infratemporal fenestra is nearly vertical. These and other structural differences clearly distinguish this taxon from all other pachycephalosaurids. *Tylocephale* seems to be most closely related to *Stegoceras* (as noted by Maryańska and Osmólska (1974)).

Prenocephale prenes is represented by an excellently preserved skull (without mandible) and some postcranial elements. This species is characterized by an extensively developed dome, a relatively long and deep snout, a large diastema between premaxilla and maxilla, the structure of the teeth and the ornamentation of the external surface of the skull. It most closely resembles *Pachycephalosaurus* from the Lance Formation of Montana, South Dakota and Wyoming in the extreme development of the dome, the closure of the supratemporal fenestrae, a relatively long snout and large diastema (Maryańska and Osmólska 1974). But the two taxa are distinguished from each other by a number of differences and I would suggest that they represent two different lines of pachycephalosaurid evolution. The dome in *Prenocephale* includes prefrontals, supraorbitals and postorbitals (aside from frontals and parietals), while that in *Pachycephalosaurus* is formed by the frontoparietal only and extends far posteriorly, abruptly ending at the posterior margin of the skull.

Homalocephale calathocercos is known from an incomplete skull and postcranial skeleton. It is characterized by its flat skull roof with large supratemporal fenestrae. Considering the fact that there are two pachycephalosaurid species from the Nemegt Formation (and the holotypes are even from the same locality), one is tempted to invoke sexual dimorphism to explain the differences. Maryańska and Osmólska (1974: 62, 100) do not accept this idea, citing a plethora of minute differences between *Homalocephale* and *Prenocephale* in structural features of the skull and postcranial skeleton. Galton (1974a,b) has demonstrated a surprisingly large amount of intraspecific variation in certain ornithopods. With the exception of three features, all differences cited by Maryańska and Osmólska (1974) can be explained as individual variation owing to differences in size or owing to the absence of the dome. However, three features definitively distinguish

Homalocephale from *Prenocephale*: the flat skull roof (with large supratemporal fenestrae), the different pattern of tooth wear and the ornamentation of the external surface of the skull. *Prenocephale* shows wear facets on the apex of the maxillary teeth (Maryańska and Osmólska 1974: 55) rather than in a medial position (as in *Homalocephale*, *Stegoceras* and most other ornithopods). The main difference in the ornamentation of the external surface of the skull is the presence of large pits on the periphery of the skull roof in *Homalocephale*.

Are the two taxa just male and female of one sexually dimorphic species (which, by page priority, would have to be named *Prenocephale prenes*)? Additional material is necessary for a final decision. A similar situation in *Stegoceras* was noted by Galton (1971: 44), who described and illustrated (Galton 1971: figs. 5 - 6) a nearly flat-roofed frontoparietal from the Judith River Formation of Alberta. Galton considered this specimen as a variant of *Stegoceras validus*, possibly a female. Given that the domed individuals are males and the flat-roofed individuals are females of the same species - is it not surprising that only one "female" has been discovered among 40 to 50 frontoparietals from the Judith River Formation of southern Alberta? Perhaps, rather than postulating marked sexual dimorphism, one should consider the possibility of a lineage of pachycephalosaurids with flat skull roofs, indicating a different type of intraspecific combat (presumably pushing as in *Amblyrhynchus* (Eibl-Eibesfeldt 1955)).

Finally, *"Troodon" bexelli* should be mentioned as the oldest record of the Pachycephalosauridae from East Asia (Bohlin 1953). This, species is based on a poorly preserved frontoparietal from the Upper Cretaceous (precise age uncertain, probably older than the Djadokhta Formation (Kielan-Jaworowska, pers. comm., 1976)) of Tsondolein-Khuduk, Inner Mongolia. Apparently it differs from *Stegoceras validus* in the few comparable features (Bohlin 1953: 32 - 33). From Bohlin's description and figures it appears that the specimen is not diagnostic and merely indicates the presence of a pachycephalosaurid at the Tsondolein-Khuduk locality. *"Troodon" bexelli* should be considered a *nomen vanum*.

B. North America

Five species of *Stegoceras* have been described from the Upper Cretaceous of Alberta, four (*S. validus*, *S. brevis*, *S. lambei* and *S. sternbergi*) from the Judith River Formation and one (*S. edmontonensis*) from the (Lower) Edmonton Formation. All these species are based on isolated frontoparietals. Gilmore (1924: 10 - 11) recognized that a large amount of variation was found in the dimensions of the frontoparietals of *Stegoceras*, "a condition that might well be expected in such [a] highly specialized structure, and which points to a wide individual variation rather than to constant specific differences" (Gilmore 1924: 11). It appears that Gilmore was the only author to recognize this point. Brown and Schlaikjer (1943: 130) recognized that *Stegoceras brevis* belongs to *S. validus* and also referred a large frontoparietal to the latter species, later designated as the holotype of *S. lambei* Sternberg, 1945. As a detailed biometrical survey of the frontoparietals of the North American Pachycephalosauridae is in progress (Dodson, personal communication, 1975), I have merely plotted a few selected dimensions for the frontoparietals of all "species" of *Stegoceras*, based on the data in Brown and Schlaikjer (1943) (with the addition of a specimen illustrated by Galton (1971: figs. 5 - 6)) (fig. 30). It appears from the diagrams that the material from the Judith River Formation of Alberta represents but one variable species, *Stegoceras validus*, with *"brevis"* and *"sternbergi"/"lambei"* as the opposite extremes. Galton's supposed specimen of *Stegoceras validus* does not fit into the *validus* "cluster", possibly indicating the presence of a second type of pachycephalosaurid from the Judith River Formation. On the basis of the diagrams I also do not hesitate to refer *S. edmontonensis* to *S. validus*, extending the record of the latter species into the Lower Edmonton Formation.

Three species of *Pachycephalosaurus*, the largest known pachycephalosaurid, have been described from the Lance Formation (Gilmore 1931, 1936 and Brown and Schlaikjer 1943). *P. grangeri* Brown and Schlaikjer, 1943 shows an extremely large dome and lacks a parietosquamosal shelf (Brown and Schlaikjer 1943: pls. 38 - 39), while *P. wyomingensis* (Gilmore, 1931) and *P. reinheimeri* Brown and Schlaikjer, 1943 have a low frontoparietal vault and a well-developed parietosquamosal shelf (see Gilmore (1931: pls. 1 - 3; 1936: figs. 2 - 3) and Brown and Schlaikjer (1943: pl. 42), respectively). The sutural contact between nasal and frontal is narrow in *P. grangeri* and *P. reinheimeri* (Brown and Schlaikjer 1943: 133 and 143, respectively), while it is broad in *P. wyomingensis* (Brown and Schlaikjer 1943: 143). There is little doubt in my mind that the specimens all

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Figure 30. (A) - (D) diagrams plotting selected dimensions of isolated frontoparietals referable to *Stegoceras*. Subdivision of axes logarithmic.

(A) height above endocranial cavity (H) versus greatest length (L).

(B) width of frontal at suture between nasal and frontal (N - FW) versus greatest width (W).

(C) greatest width (W) versus greatest length (L).

(D) median thickness of frontals at sutural contact with nasals (T) versus greatest length (L).

Data from Brown and Schlaikjer (1943).

Symbols: v - *S. validus* (*v* - type specimen of *validus*)

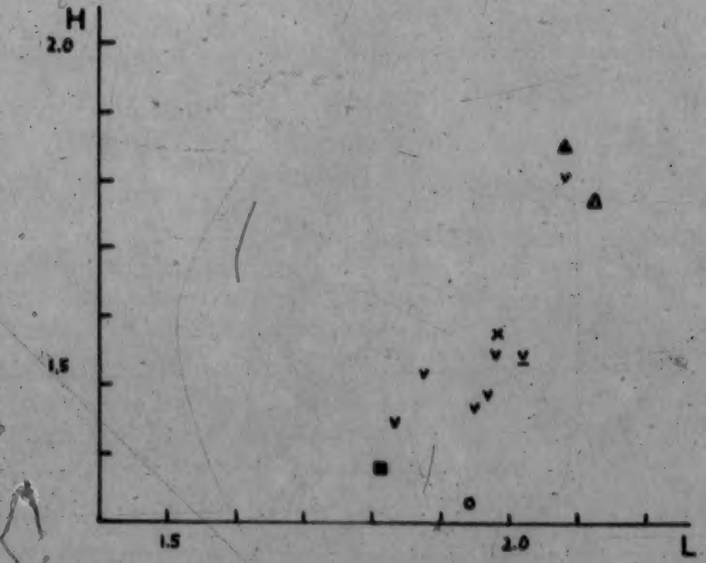
x - *S. "edmontonensis"*

■ - *S. "brevis"*

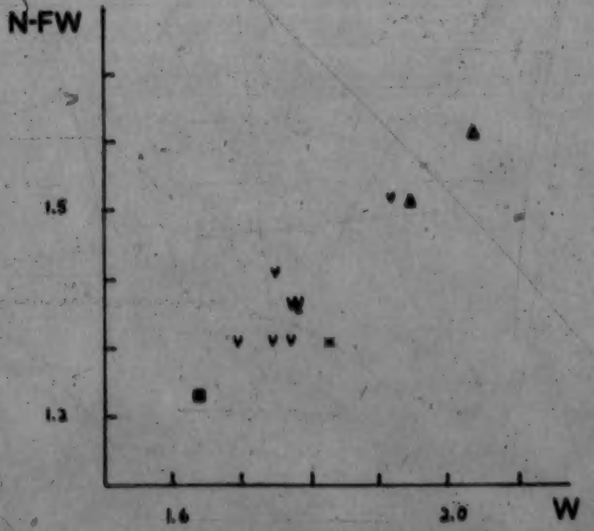
▲ - *S. "lambei"*

Δ - *S. "sternbergi"*

o - *S.* sp. (for Galton (1971: figs. 5 - 6))



A



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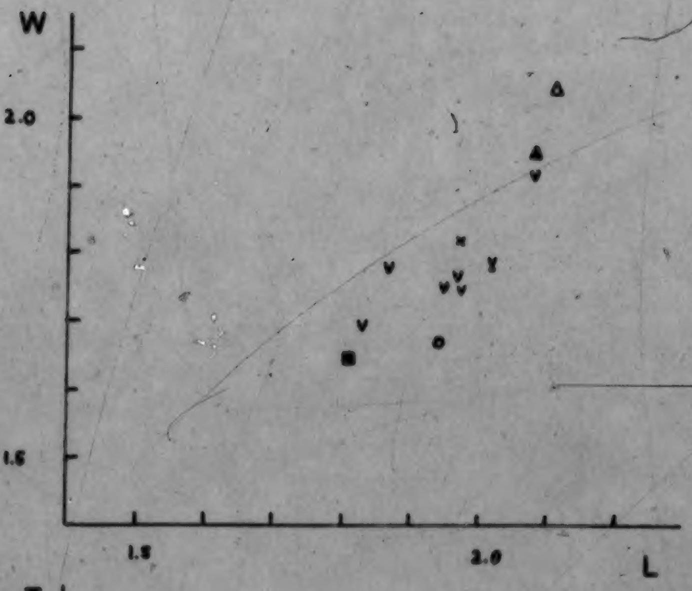

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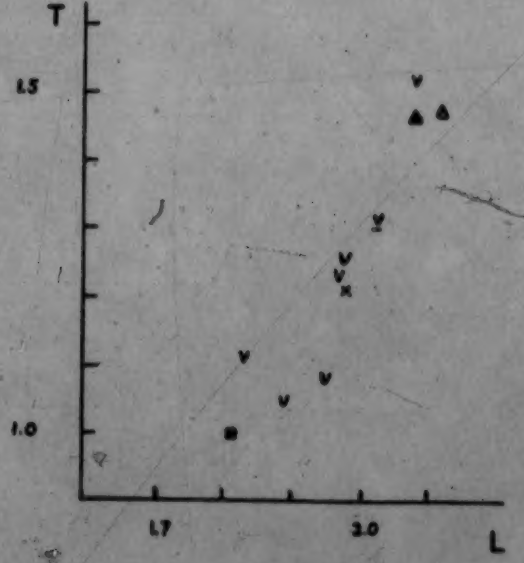

D

represent but one species, *P. wyomingensis*.

Pachycephalosaurus can readily be derived from *Stegoceras* (Brown and Schlaikjer 1943: 146) by the following changes:

1. increase in size;
2. further thickening of the skull roof and obliteration of the supratemporal fenestrae;
3. development of an ornamentation consisting of large nodes;
4. shortening of the basicranial region;
5. increase in the number of maxillary teeth;
6. reduction in the size of the foramen magnum;
7. more ventral orientation of the occipital condyle and foramen magnum;
8. face narrower and longer.

A third type of pachycephalosaurid, which differs from *Stegoceras* and *Pachycephalosaurus*, is documented by a large frontoparietal from the Judith River Formation of Alberta, now housed in the Provincial Museum and Archives of Alberta, Edmonton (Galton, personal communication, 1976). No further comments are included here as a detailed account by Galton and Wall will soon be published.

2. Diagnosis of *Stegoceras*

The increase of our knowledge about the Pachycephalosauridae since the publication of Gilmore's (1924) account makes a new definition of the genus *Stegoceras* necessary. Many of Gilmore's diagnostic characters have since been shown to be diagnostic of the family

Pachycephalosauridae and the supposed presence of abdominal ribs was based on a misinterpretation.

Consequently, I propose to characterize the genus *Stegoceras* as follows:

> Medium-sized pachycephalosaurid. Cranial roof thickened, often highly elevated. Parietosquamosal shelf developed. Infratemporal fenestra narrow, long and sloping anteroventrally. Quadrate sloping anteroventrally. Occipital region wide. Snout foreshortened and deep. Supratemporal fenestrae reduced. Posterior process of premaxilla short. Short diastema between premaxillary and maxillary teeth. No caniniform teeth in the dentary. Premaxillary and anterior dentary teeth incisiform. Dental formula: $\frac{\text{pmx. } 3 + \text{mx. } 16}{\text{de. } 17}$.

3. The origin of the Pachycephalosauridae

As Galton (1972: fig. 3) correctly recognized, the Pachycephalosauridae were probably derived from the Hypsilophodontidae during the Middle or Upper Jurassic. *Yaverlandia* is the earliest known pachycephalosaurid, known from a frontal region from the Lower Cretaceous (Wealden) of the Isle of Wight. It shows a small dome on each frontal. The frontal still participated in the formation of the dorsal rim of the orbit, excluding the postorbital from contact with the prefrontal. Supratemporal fenestrae were still large and well-developed. The dorsal surface of the frontal shows an irregular pitting. The orbitosphenoid was well-ossified. The orbit was still visible in dorsal view. The olfactory lobes were not enclosed by bone ventrally. *Yaverlandia* is but little advanced beyond the hypsilophodontid level of structural organization, mainly differing from the hypsilophodontids in the degree of ossification of the orbitosphenoid and the beginning thickening and ornamentation of the frontal.

Hypsilophodon represents a suitable model for an ancestor although being too late (contemporaneous with *Yaverlandia*) to be a pachycephalosaurid ancestor itself. Using distortion grids for facile visualization of the proportional changes in the skull occurring in a lineage *Hypsilophodon* - *Stegoceras*, the following changes can be observed (fig. 31):

1. Increase in thickness of the frontoparietal region, resulting in alteration of the topographical relationships with the surrounding elements and reduction of the supratemporal fenestrae;
2. anteroventral inclination of the occipital region, the suspensorium, and the infratemporal fenestrae;
3. shortening and deepening of the face;
4. shift of the orbit to a more ventral position (no longer visible in dorsal view).

Several anatomical changes occur in the cranial architecture in the structural sequence *Hypsilophodon-Yaverlandia-Stegoceras*. In *Hypsilophodon* the orbitosphenoid was presumably cartilaginous (Galton 1974a: 27), whereas it was a thin plate of bone not sutured to the

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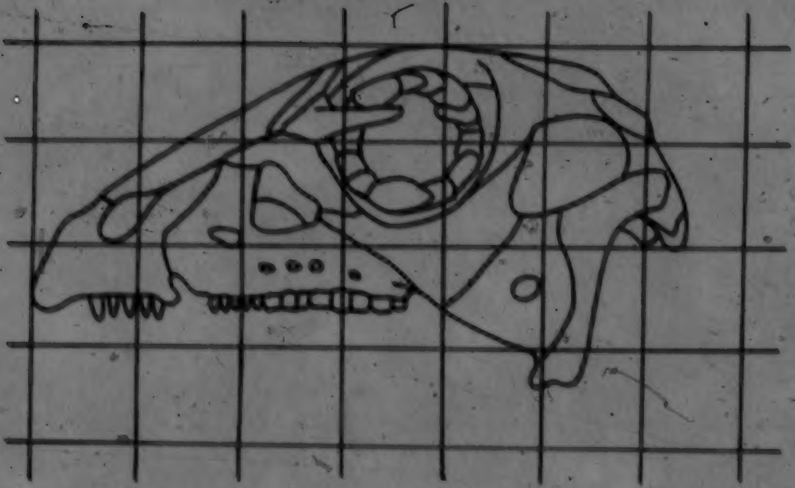
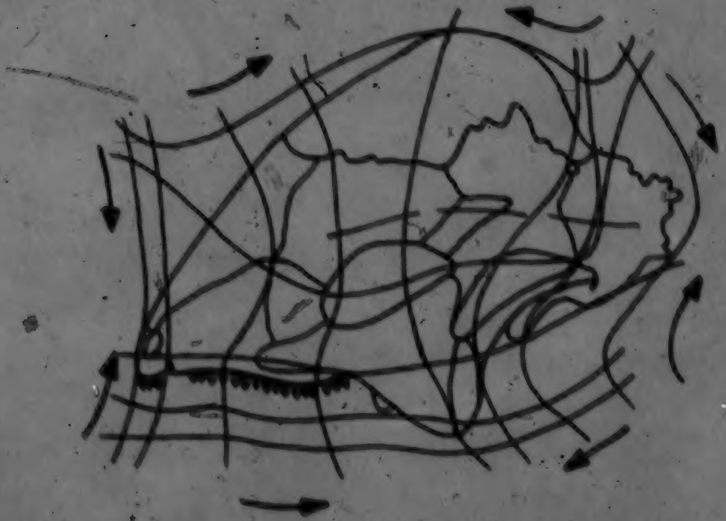
Figure 31. Distortion grids visualizing the proportional changes during the derivation of a pachycephalosaurid skull (*B*, *Stegoceras*) from a hypsilophodontid skull (A, *Hypsilophodon*). Outline in (A) after Galton (1974a: fig. 3).



A



B

frontal in the Upper Cretaceous hypsilophodontid *Parksosaurus*. In *Yaverlandia* and all other pachycephalosaurids the orbitosphenoid is well-ossified and firmly sutured (Galton 1971, Maryańska and Osmólska 1974, and personal observation). The supraorbital, still free in *Hypsilophodon* (Galton 1974a: fig. 3), fuses with the prefrontal in the Pachycephalosauridae. The olfactory lobes become ventrally enclosed by bone in *Stegoceras* and other advanced pachycephalosaurids (but not in *Yaverlandia* (Galton 1971 and personal observation)).

There are no difficulties preventing a derivation of the Pachycephalosaurid[illegible] from the Hypsilophodontidae during the Jurassic. Maryańska and Osmó[illegible] (1974: 101) think that this derivation took place earlier, perhaps during the Triassic, arguing that the later hypsilophodontids show cursorial adaptations while pachycephalosaurids do not. I disagree with this point of view as already the earliest known ornithischians, the Fabrosauridae (Thulborn 1972) and Heterodontosauridae (Bonaparte 1976, Santa Luca, Crompton and Charig 1976), are highly cursorial and the Hypsilophodontidae gave rise to several other non-cursorial groups of the Ornithischia (Iguanodontidae *s.l.*, Hadrosauridae, Ceratopsia and Ankylosauria (?)) and even include non-cursorial species themselves (*Dryosaurus altus* (Marsh, 1878) and *Dysalotosaurus lettowvorbecki* Pompeckj, 1920 from the Upper Jurassic of the U.S.A. and Tanzania, respectively). The absence of premaxillary teeth in the latter (Janensch 1955) seems to preclude them from the ancestry of the Pachycephalosauridae.

4. The systematic position of the Pachycephalosauridae

The classification of the Pachycephalosauridae within the Ornithischia has been a matter of controversy and is still open to discussion. First, only a few tantalizing frontoparietals were available. Later, the collection of more complete materials helped to solve certain problems but also created new questions yet to be solved.

In his original description of *Stegoceras validus*, Lambe (1902: 68) discussed this species in the section "Ceratopsidae" of his monograph. Subsequent authors assigned *Stegoceras* to the Ankylosauria (the latter being included in the Stegosauria or Thyreophora by these early workers; see Introduction for details). Gilmore (1924: 39) put *Stegoceras* in the Ornithopoda and most later authors (with the exception of Nopsca) accepted this reference. Recently, however, a few authors have raised doubts about the validity of Gilmore's classification: Rozhdestvensky (1964: 588) listed the Pachycephalosauridae as *incertae subordinis* and, more recently, Coombs (1971: 430) suggested that "possibly the family should be classified as Ornithischia *incertae sedis* until more is known about them." Rozhdestvensky (1972) even referred the Pachycephalosauridae again to the Ankylosauria!

Maryańska and Osmólska (1974) reconsidered the problem on the basis of the new Mongolian materials. They transferred the Pachycephalosauridae to a new suborder Pachycephalosauria, admitting (1974: 49) that it could be regarded as an infraorder of the

Ornithopoda. A number of characters distinguishes the pachycephalosaurids from the typical ornithopods as defined by Romer (1968: 627):

1. absence of a contact between premaxilla and lacrimal;
2. tendency for closure of the supratemporal fenestrae;
3. vertical extension of the occipital region;
4. ossified *lamina orbitonasalis* and *planum supraseptale;*
5. thickened frontoparietal region;
6. quadratojugal descending very close to the mandibular articulation of the quadrate;
7. shortened basicranium;
8. presence of an "epipterygoid" (at least in *Prenocephale*);
9. lack of an obturator process on the ischium;
10. exclusion of the pubis from the acetabulum;
11. articulation of sacral ribs 2 and 3 with the ischium (at least in *Homalocephale*);
12. tongue-and-groove type of interzygapophyseal articulation on (at least) the posterior dorsal vertebrae;
13. long caudal ribs.

It should be noted that not all of the characters listed above are documented for all pachycephalosaurids but the rather uniform organization of comparable skeletal elements suggests the presence of these features throughout the group. A character used as unique in earlier definitions of the family was the presence of "abdominal ribs", which since have been shown to represent fragments of caudal tendons.

Unique characters of the Pachycephalosauridae are no. 4, 5, 8, 11, 12 and 13.

Character 1 is shared by *Scelidosaurus* (probably an early ankylosaur (Charig, personal communication, 1976)), *Psittacosaurus* (Coombs 1971: 413), *Stegosaurus* (Marsh 1896: pl. 48, fig. 3 and Gilmore 1914: fig. 3), some ceratopsians (Lull 1933: figs. 38 - 39), protoceratopsians (Maryańska and Osmólska 1975: fig. 6) and the ankylosaur *Pinacosaurus* (Coombs 1971: 413).

Character 2 is also found in the ankylosaurs where the closure of the supratemporal fenestrae is also accomplished by the surrounding bones (Maryańska *in* Coombs 1971: 157) (and not, as previously suggested in the literature, by fusion of the dermal armor plates to the skull roof).

Character 3 is present in a similar fashion in the Ceratopsia but in the latter the basicranial region is not in the same plane as the occipital region.

Characters 6 and 7 are more markedly developed in pachycephalosaurids and are approached by some ornithopods.

Character 9 is shared by the Stegosauria (*Stegosaurus;* Marsh 1896: pl. 43, fig. 1 and Gilmore 1914: fig. 42), some ceratopsians (*Brachyceratops;* Gilmore 1924: fig. 3B), protoceratopsians (Brown and Schlaikjer 1940: fig. 31 and Russell 1970: fig. 1), *Psittacosaurus* (Osborn 1924: fig. 8) and Ankylosauria (Ostrom 1970: pl. 25, fig. G and Charig 1972: fig. 2 and pl. 6, fig. A).

Character 10 is developed in a somewhat similar fashion in some ankylosaurs; the pubis in these forms is also strongly reduced and almost completely excluded from participating in the formation of the acetabulum (Charig 1972: fig. 7B).

Two other similarities between the Pachycephalosauridae and the Ceratopsia have been noted by Maryańska and Osmólska (1974) and Gilmore (1924). The ischia of *Homalocephale* and *Stegoceras* resemble those of the Ceratopsia (but not Protoceratopsidae) in being decurved in a gentle arch. The resemblance in the curvature of the ischia seems to be of doubtful significance. The endocranial cast of *Pachycephalosaurus* (Brown and Schlaikjer 1943: 140 and pl. 41) shows some resemblances to the endocranial casts of ceratopsians (Brown 1914), *e.g.*, in the double flexure of the brain (*i.e.*, the long axes of the myelencephalon and the olfactory stalks are parallel to each other). The structure of the ornithischian brain is extremely uniform (Brown 1914, Ostrom 1961 and Coombs 1971) and appears to be of little (if any) value in establishing relationships within the Ornithischia.

The lack of a premaxilla - lacrimal contact and of an obturator process also appears to be of little value in supporting closer relationships to either ankylosaurs or ceratopsians, also being present in stegosaurs and *Psittacosaurus*. Unless one assumes that all these groups are very closely related to each other (an assumption that is not supported by the fossil record), there is no good evidence establishing close relationships of the Pachycephalosauridae to either Ankylosauria or Ceratopsia.

Two alternatives are available for the classification of the Pachycephalosauridae: either reference to a suborder of their own (as proposed by Maryańska and Osmólska (1974)) or a more flexible definition of the Ornithopoda. After the removal of the Psittacosauridae from the Ornithopoda (Maryańska and Osmólska 1975) the latter solution is possible. The differences between the Pachycephalosauridae and Hypsilophodontidae are less numerous than those between the latter and the Ceratopsia, Ankylosauria or Stegosauria. I do not think that separation of the pachycephalosaurids at the subordinal level is warranted and a subdivision of the Ornithopoda at the infraordinal niveau must await a revision of the whole group. At the present time I follow Galton (1972: 465) in placing the Pachycephalosauridae in the Ornithopoda.

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